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A CONTRIBUTION TO THE LIFE HISTORY OF IMPATIENS SULTANI

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(WITH PLATES XIV, XV)

This paper is based upon a study of slides made through a series of years for class use in the Botany Department of Wellesley College. The material was taken from greenhouse plants of the rose or bright pink variety of *Impatiens Sultani* Hook. The bright red and light pink varieties also were growing in the greenhouse, but care was taken to collect material from the rose-flowered plants only. Some of the plants from which the flowers were collected were chance seedlings. No attempt was made to determine whether or not these were a pure strain of the rose-colored form. In BAILEY'S (4) *Standard Cyclopedia of Horticulture* the original form of *I. Sultani* is given as a rich scarlet, shades ranging from pink to almost purple being found on hybrids or sports. If this be true, then all the rose-colored forms used for this study are either hybrids or sports.

According to BAILEY the species *I. Sultani* was originally found in Zanzibar and named by HOOKER in honor of the Sultan of Zanzibar. In ENGLER and PRANTL'S *Die Natürlichen Pflanzenfamilien* (16) it is cited from Sierra Leone, Western Africa. It is stated in GRAY'S *Manual* that the Balsaminaceae often contain two kinds of flowers, the large showy ones which rarely ripen

seeds, and small ones which are cleistogamous. *I. Sultani* is not given by ENGLER and PRANTL in their list of species containing cleistogamous flowers, and I was unable to find any cleistogamous flowers on the many plants of this species which were investigated.

The material fixed ranged from very small buds to young fruits. In preparing the buds for fixing, the smallest ones were put up entire; the sepals and petals were removed from all others; and in the largest buds the pistil and stamens were separated. From the flowers and the fruit only the ovaries were preserved and these were trimmed slightly at the angles to allow more rapid penetration of the fixer, which in all cases was Flemming's chromo-acetic solution. In general, the material was sectioned longitudinally and stained with Flemming's triple stain.

Ovary

The ovary consists of 5 carpels with axial placentation. There are several ovules in each loculus and the age of the ovules in a given loculus advances from base to apex, the youngest being at the base of the ovary. At the time when the microspore mother cells are in prophase of the heterotypic division the ovules appear as slightly curving outgrowths from the placenta, with or without any indication of the inner integument (fig. 1). It is apparent that the ovules of *I. Sultani* occur earlier in relation to the development of the anthers than is the case in many other plants. Miss BLISS (**8**) reports that in *Viola* the ovule initials cannot be detected when the microspore mother cells are in the prophase of the heterotypic division, and similar observations have been made by many other investigators.

As the inner integument begins to appear, a single hypodermal archesporial cell becomes differentiated at the apex of the nucellus (fig. 2). *I. Sultani* agrees with *I. pallida* (Miss RAITT **37**) in having but the one archesporial cell, but differs from that species in having no parietal cell cut off from the archesporial cell. According to COULTER and CHAMBERLAIN (**15**) there is a general tendency to suppress the parietal tissue among monocotyledons and Archichlamydeae. "The suppression of parietal tissue among Archichlamydeae is most extensively displayed by the Ranunculaceae

and its allies rather than by the more specialized groups." Balsaminaceae, one of the higher groups of the Archichlamydeae, shows complete suppression of parietal tissue in *I. Sultani;* in *I. pallida,* however, Miss RAITT (**37**) describes a parietal cell, but her illustrations are not very conclusive.

From the first the megaspore mother cell is the only hypodermal cell at the apex of the ovule. It is surrounded by the epidermis of the nucellus at its sides and apex, and is bounded by several nucellar cells at its base (fig. 2). The cell is slightly longer than wide and extends almost to the plane of insertion of the inner integument. It keeps pace with the growth of the ovule and continues to occupy all of the nucellus within the epidermis except in the chalazal region. As growth continues it changes from a broad cell to a long narrow one (figs. 2–4, 6).

The nucleus of the megaspore mother cell contains one nucleolus which at first is separated from the chromatic network by a clear area (fig. 2). As division is initiated, the chromatic reticulum forms a more or less complete spirem, separates from the nuclear membrane, collects about the nucleolus, and enters the synaptic stage (figs. 3, 4). On recovery from synapsis the spirem spreads out into the nuclear cavity and very soon exhibits the second contraction stage (fig. 5) similar to that which has been described for *Lilium* and several other angiosperms by ALLEN (**2**), MOTTIER (**32**), and others. According to OVERTON (**35**), this phenomenon does not occur among the majority of the angiosperms.

During this stage the spirem is thick, and at places uneven and massed. Here and there, in the less condensed areas, light streaks show, suggesting either a longitudinal splitting of a single spirem or an approximation of two. The contracted spirem is in contact with the nuclear membrane at several points, but the greater amount of the chromatic material is near the nucleolus at the center of the nucleus. At this time the nucleus is near the micropylar end of the megaspore mother cell. About midway between it and the chalazal end are numerous fibers with blue staining dots scattered among them. This characteristic has been observed in several megaspore mother cells, but its significance was not determined. These fibers played no apparent rôle in the formation

of the spindle or in the development of the cell wall, since they disappear before the first division. However, they may represent an early assembling of the kinoplasmic substance preparatory to spindle formation.

Fig. 6 shows the spirem partially segmented with the nucleolus near the center of the cavity and the segments projecting in from the nuclear membrane. Later the chromosomes become very short and group themselves about the nucleolus (fig. 7). At this time they suggest the tetrads described for many animals and closely resemble those of *Arisaema triphyllum* as figured by ATKINSON (3). A typical bipolar spindle is formed and the bivalent chromosomes when arranged at the equatorial plate appear as very short X's, V's, and Y's.

Two cells separated by a distinct cell wall result from the heterotypic division and form the axial row (fig. 8). The micropylar cell of this row is smaller than the other, and disintegrates very quickly. The chalazal cell grows and is the mother of the embryo sac. An axial row of two cells is not common among the Archichlamydeae. TREUB (43) describes an axial row of two cells for *Viscum articulatum*, and several cases have been reported among the monocotyledons. Miss RAITT (37) states that 4 megaspores are formed in *I. pallida*, but makes no sketch showing them. In her fig. 1, *J*, she shows an ovule containing a large cell which she names the functional megaspore. Between it and the epidermis a small disintegrating cell appears. The sketch closely resembles the appearance of the ovules of *I. Sultani* with an axial row of 2 cells and throws doubt upon her assertion that there is an axial row of 4 cells.

The micropylar cell of the axial row is never large, and is so short-lived that it is easily overlooked, and the embryo sac seems to arise directly from the megaspore mother cell, as in *Lilium*. As the micropylar cell disintegrates and the epidermal cells of the nucellus grow, there appears simply a small blue staining cavity between the embryo sac mother cell and the apical region of the epidermis, as cited by COULTER and CHAMBERLAIN (15) for *Clematis*, and *Helleborus* (GUIGNARD 20), and *Delphinium* (MOTTIER 31). The chalazal cell grows and its nucleus divides, completing the

reduction division and giving rise to the 2-nucleate embryo sac (fig. 9). At this stage there is still something of the disintegrating micropylar cell to be seen, but at a slightly later stage it has entirely disappeared (fig. 10). The embryo sac is thus derived from two megaspores as in *Viscum articulatum* (TREUB **43**) of the Archichlamydeae and in *Trillium* (HEATLEY **26**) and several other monocotyledons.

The two megaspore nuclei move to the opposite poles of the sac and divide (fig. 10). At this stage the sac is vacuolate and continues so until a late 4-nucleate stage (figs. 11–13). The 8-nucleate stage follows rapidly upon the four. Two-, 4-, and 8-nucleate stages have all been found in the same ovary, the 2-nucleate stage being at the base of the loculus. It is very easy, in serial sections, to confuse an early 8-nucleate stage with a late 4-nucleate stage, as the sacs have the same shape and cytoplasmic appearance.

In *Eriocaulon septangulare* (SMITH **40**) the central vacuole first appears at the 4-nucleate stage. In *I. Sultani* the late 2-nucleate sac is vacuolate with large vacuoles between the two nuclei, but there is not one large central vacuole until the female gametophyte has been organized (figs. 10–14, 17). In an early 4-nucleate stage there are several large vacuoles extending along either side of the row of nuclei (fig. 11). During the 4-nucleate stage the sac enlarges, the cytoplasm becomes more dense, and the large vacuoles decrease (figs. 12, 13). By the time the 8 nuclei are formed the cytoplasm is very dense and contains a large amount of stored food, and the vacuoles have become small and inconspicuous (fig. 14). Very soon, however, a large central vacuole appears (fig. 17). The time of the inception of this central vacuole varies considerably. It may arise while the antipodal polar is at the base of the sac, or it may not appear until the polars are in contact and near the egg (figs. 14, 17, 18).

After the organization of the 8 nuclei the egg apparatus soon forms. The egg is more or less pear-shaped, with the larger end extending down below the synergids. The nucleus and greater part of the cytoplasm are in this region and the narrowed part extends up back of the synergids and is vacuolate. It evidently

resembles the egg of *Aster novae-angliae* (CHAMBERLAIN **12**) and that of many other plants as to shape and relation of nucleus and cytoplasm (fig. 17).

The nuclei of the synergids do not always have the same position (figs. 15–17, 19). In the youngest sac of the series (fig. 15) there is a large vacuole at the base of either synergid, with the nucleus above and near the micropylar end. Fig. 16 illustrates a condition in which the synergid nuclei have moved down halfway, and in one cell there is a vacuole on either side of the nucleus, while in the other there is a large vacuole below it but only a small one above it. In fig. 17 one nucleus has moved entirely below the vacuole and is near the membrane at the end of the cell, whereas the other nucleus is still between two or more vacuoles. In a much older embryo sac (fig. 19) the synergids are longer, the nucleus of each is at its base, and a large vacuole appears above the nucleus. At all stages in the growth of the egg apparatus the synergids contain a fairly dense cytoplasm at the apex. It seems clear that the position of the synergid nucleus varies in relation to the age of the sac; that at first it is near the micropylar end of the synergid and above the vacuole; that later it passes the large vacuole and moves down to the opposite end of the cell. When the egg apparatus is mature the two nuclei are at the base of the cells, near the egg nucleus, and just below the large vacuoles (fig. 19).

According to the literature on the subject the position of the synergid nuclei in different plants may vary in relation to the large vacuole of the cell, but I have found no suggestion that the variation in a given species represents different stages in development. CHAMBERLAIN (**12**) gives the situation of the nuclei in *Aster novae-angliae* as varying in position from one end of the cell to the other but most frequently near the middle, the large vacuole being usually at the chalazal end of the synergid. GUIGNARD (**19**) says that in the Leguminosae the vacuole is usually at the base of the cell and the nucleus is central, but the vacuole may sometimes be above the nucleus. BARNES (**6**) in *Campanula americana*, GUIGNARD (**24**) in *Hibiscus Trionum*, and STRASBURGER (**42**) in *Wikstroemia indica von Buitenzorg* find the nucleus above the

vacuole; while PACE (**36**) finds the synergid vacuoles of *Parnassia* in various positions.

The antipodals are surrounded by denser cytoplasm than is present above them, and they appear rarely as separate cells with delicate walls separating them (fig. 18), or, as is more commonly found, the mass of cytoplasm with the 3 nuclei is more or less cut off from the rest of the sac by a membrane but the cells are not separated. In either case they are but short-lived and disappear soon after the egg apparatus is formed. The embryo sac then persists for a long time with but 5 nuclei. Miss RAITT says that the antipodals in *I. pallida* cannot be distinguished with certainty and are evidently transitory. This ephemeral nature of the antipodals is common among many of the angiosperms. In *Striga lutea* (MICHELL **29**) the 3 antipodal cells begin to disintegrate before fertilization. In *Richardia africana* (MICHELL **30**) the disintegration is somewhat earlier, evidently more nearly like *I. Sultani*. In this species the antipodals were never found to increase in size or number and grow into the adjoining tissue, as has been described by CHAMBERLAIN (**12**) and OPPERMAN (**34**) for *Aster novae-angliae* and by others for various plants.

Very quickly after the 8 nuclei of the sac have been formed the antipodal polar moves up toward the micropylar polar and the 2 nuclei remain near each other at a short distance below the egg nucleus for some time. The nuclei may or may not be spherical, but they always contain a prominent nucleolus with a small highly refractive spot at the center. The chromatic substance of the polar nuclei is small in amount and forms either a delicate network lying just within the nuclear membrane, or a few strands radiating out from the nucleolus. Most of the food stored in the sac at an earlier period disappears before the female gametophyte reaches maturity and the sac becomes very vacuolate, with only a layer of cytoplasm at its periphery and surrounding the nuclei in the micropylar half of the sac (fig. 37).

During the later development of the embryo sac its shape becomes much changed (figs. 17, 19, 37). While the antipodals are still present the sac is a little over three times longer than wide, with the micropylar and antipodal ends both rounded in outline

(fig. 17). After the antipodal cells disintegrate the basal region of the sac grows down into the chalaza. The growing portion is blunt or more or less triangular in outline, and but little narrower than the sac just above. The antipodal growth continues until the sac is over five times as long as it is wide (fig. 19). Following the development of this antipodal haustorium the sac widens in the region of the polar nuclei and assumes its mature shape (fig. 37).

During the origin and development of the female gametophyte the megasporangium has been undergoing marked changes. The ovule begins to curve before the megaspore mother cell appears, and by the time its nucleus has reached the segmented spirem stage the ovule has attained the anatropous position. At this time the inner integument extends beyond the nucellus and forms a fairly deep micropyle (figs. 1–4, 6). The outer integument arises from the lower two-thirds of the inner integument, appearing as a swelling from the outer part of the latter (fig. 6). This swelling increases greatly in breadth and grows up until its apex is on a line with the tip of the inner integument. It never grows beyond this point to aid in forming the micropyle, and the two integuments become distinct only at the summit (figs. 9, 37).

The origin of the outer integument in *I. Sultani* differs from the majority of plants and from the other species of *Impatiens* that have been studied. Miss RAITT (**37**) in *I. pallida* and GUIGNARD (**22**) in *I. parviflora* both show the outer integument arising from the basal portion of the ovule and remaining throughout its length distinct from the inner. As a result of his study of *I. balsamina*, BRANDZA (**9**) states that the Balsaminaceae have but one integument, but BRUNOTTE (**10**) disagrees with BRANDZA and gives two integuments for this family. According to LONGO,[1] as cited by Miss RAITT, this is the rule for the genus *Impatiens*, but the origin of the outer integument and its extension at the micropylar region appear to vary. From my study of the ovule of *I. Sultani* it can readily be seen how BRANDZA thought there was but one integument if *I. balsamina* is similar to *I. Sultani* in having the outer integument an outgrowth of the inner integument with only their tips free.

[1] LONGO, B., Richerche su le *Impatiens*. Annali Bot. **8**:65–77. 1909.

In *De l'ovule*, WARMING (**45**) notes a few exceptions to the usual order of development of the integuments and gives *Viola*, *Ficus*, *Convallaria*, and *Orchis* as having two integuments which appear to grow as a single organ, and *Tropaeolum* as having at first two integuments which later appear as one. WARMING quotes STRASBURGER as saying that in *Delphinium* the integuments originate as one and elevate themselves as a unit; later at the summit the two integuments become distinct. Judging from his figure the conditions in *Delphinium* are much the same as in *I. Sultani*.

As given earlier, the megaspore mother cell when it arises is completely surrounded, except at its base, by the epidermis of the nucellus, and the developing embryo sac also continues to lie in direct contact with the epidermis (figs. 2–4, 6, 8, 9). During the 2-nucleate stage of the embryo sac the epidermis begins to break down. The disintegration first appears as a flattening of the cells and nuclei just below the apex, and then extends gradually to the base of the embryo sac (figs. 9, 10, 14, 37). In *Oxalis corniculata*, according to HAMMOND (**25**), the epidermis, which in this case serves as a tapetum, begins to disintegrate before the 2-nucleate embryo sac is formed.

The apical cells of the epidermis are often longer-lived than those just below them, for it is quite common to find two or three cells surmounting the embryo sac and connected by only a line with those still persisting about the center of the sac (fig. 12). A somewhat similar appearance has been described by SMITH (**40**) for *Eriocaulon septangulare*, where "the nucellar tissue lateral to the megaspores breaks down and is absorbed by the growing embryo sac. A few of the apical cells of the nucellus persist for a long time and enlarging assume the appearance of a tapetum. These too are ultimately absorbed and the embryo sac abuts directly upon the inner integument and micropyle." In *I. Sultani*, however, these apical epidermal cells do not enlarge and seem to have no special function.

While the epidermis continues to disappear it leaves but a line around the upper half of the sac (fig. 10). As the disintegration progresses downward, the cells near the base of the sac possess their normal tabular shape, while those nearer the middle of the

sac are narrowed and pointed. The nuclear substance in the pointed cells is dense, the nuclei are often flattened, and the cell content stains but slightly. The pointed end of the layer often becomes free from the embryo sac (fig. 13). As this layer is disappearing it is not always in close contact with the tapetum (fig. 10), and I infer that the disappearance of the epidermis is due, not to its being crushed between the tapetum and the enlarging embryo sac, but rather to the fact that it is being absorbed by the embryo sac. The basal portion of the epidermis continues to exist until after the 8-nucleate sac is formed (fig. 14).

Not only is the entire epidermis absorbed eventually but the nucellus beneath the embryo sac also. During the early stages in the development of the embryo sac the cells of this part of the nucellus are similar to those of the interior of the integuments, but beginning with the 4-nucleate stage, or occasionally earlier, they become stringy in appearance, with their long diameters in line with that of the sac. This strand of cells extends down to the chalaza which is composed of a tissue of regular, compact, densely staining, isodiametric cells (figs. 12, 14, 37). Many of the nuclei of the "stringy" cells show signs of disintegration. They become dense, lose their rounded outline, and appear elongated. These cells are bounded at the sides by the tapetum (fig. 14). The antipodal region of the sac absorbs this tissue and pushes down to the nutritive cells of the chalaza, thus completing the absorption of the entire nucellus (fig. 37). *I. Sultani* agrees with *I. parviflora* (GUIGNARD **21**) and *I. amphorata* (LONGO **28**) in having the embryo sac absorb the nucellus and thus come in contact with the micropyle and the inner integument. These species of *Impatiens*, therefore, agree with the Compositae (GOLDFLUS **17**) in the early disappearance of the nucellus.

As described by GUIGNARD (**22**), RAITT (**37**), LONGO (**28**), and BRUNOTTE (**10**) for *Impatiens*, and by others for various angiosperms, the epidermis of the inner integument forms the tapetum of regular tabular cells, which, in *I. Sultani*, extend from the base of the micropyle to a considerable distance below the base of the developing embryo sac (figs. 9, 10, 14). The tapetum loses its uniform character as early as the 2-nucleate stage of the embryo sac, when a densely staining substance appears between the tapetal

cells near the base of the micropyle and the contents of these cells stain diffusely. This appearance also extends out laterally and at this time up to the tip of the inner integument (fig. 9). The cells are crowded and their cytoplasm and nucleoplasm stain so diffusely that no attempt was made to represent their appearance in a sketch. As will be seen later, these cells break down during endosperm formation, and this doubtless represents an early stage in their disintegration. This characteristic progresses chalazally in the tapetal cells as the embryo sac develops and reaches the basal cells during early endosperm formation.

In an 8-nucleate stage the lower half of the tapetum is still normal and contains a decidedly granular cytoplasm and nucleoplasm which suggests the presence of food particles. This granular appearance is not visible in the cytoplasm of the other cells of the inner integument, although they stain more densely than do those of the outer integument. GUIGNARD (**22**) says that a nitrogenous substance accumulates in the tapetal cells of *I. parviflora* and that in all of the Balsaminaceae there is this proteid layer of tabular cells.

BILLINGS (**7**) believes with most students that the tapetal layer, whether from the inner integument or the nucellus, serves a nutritive function, dissolving and absorbing nutriment from the surrounding integument, and that its function is not simply protective, as given by HEGELMAIER (**27**). VANDENDRIES (**44**) in a study of the Cruciferae finds the tapetum a part of the inner integument, but believes it plays only a protective function. One reason given is that in the antipodal region, where the tapetum is separated from the sac by a small mass of nucellar cells, it presents the characteristic appearance of young and active tissue. This reasoning does not seem conclusive to me, since it may well be that this was a region of considerable food and that here the active cells of the tapetum digested and absorbed it and then passed it up to the embryo sac. In *I. Sultani* the tapetum persists longer at the antipodal end and it is here that growth takes place until the sac reaches the chalaza and passes slightly beyond the end of the tapetum.

BALICKA-IWANOWSKA (**5**) studied certain "Gamopetales" and described the tapetum. In agreement with CHODAT (**13**) and most recent writers, he does not believe that the tapetum is for protection,

as it is wanting in the vicinity of the haustorium, which does not possess cell walls and would therefore appear in need of protection. He thinks that the tapetal cells possess a ferment in their mucilaginous content and exercise a digestive function, for they persist while the neighboring tissue disintegrates, and they surround the parts which are in the process of rapid growth.

Extending through the raphe is a strand of cells which is surrounded, except at the ends, by a layer of cells with cutinized walls. This strand terminates at the chalaza in the tissue of regular compact cells. It is into this that the antipodal region of the sac pushes (fig. 37). In looking at the figure it will be seen that the outer layer of cutinized cells ends just as it passes this area, and on the inner side the layer ends almost in contact with the antipodal end of the tapetum. It thus forms a protective covering to the conducting tissue as it passes to the chalazal haustorium. No true vessels were ever observed in this strand of conductive cells.

As noted earlier, the antipodal nuclei disappear before the haustorium develops, thereby giving rise to the unusual condition of a haustorium unaccompanied by nuclei. In none of the literature studied was I able to find any record of a similar condition. In the cases where a haustorium has developed at the antipodal region before fertilization had occurred, it is usual for the antipodal nuclei to be present in the haustorium formed. An interesting example of this is given by SOUÈGES (41) for the Solanaceae, where a pocket is formed at the basal part of the embryo sac and the antipodals take their place in the bottom of this and their digestive juices diffuse into the tissue beneath and dissolve out a cavity. The process of dissolution of the tissue varies among the different members of the family from a simple disjunction of the digestive layer of cells to a chalazal cavity whose capacity is comparable to that of the embryo sac itself, as in *Lycopersicum esculentum*.

Stamen

The flower possesses 5 stamens whose anthers are connivent and form a hood over the pistil. In a cross-section of a bud the sides of two adjacent anthers show as having their cells in contact, and this region appears as solid tissue. Each anther contains 4 micro-

sporangia. Fig. 20 shows a cross-section of one-quarter of an anther when the nuclei of the microspore mother cells are in the synaptic state. The walls of the cells of the epidermis are cutinized and thicker than those of the other cells. The wall of the microsporangium consists of two distinct regions, the outer irregular portion made up of 1–5 layers of nearly isodiametric cells, and an inner region about 2 cells thick, the cells of which are flattened tangentially. This flattening, doubtless, results from the pressure caused by the growth of the archesporial and tapetal cells.

The microspore mother cells are separated from this inner wall by the tapetal cells. The latter, however, are not limited to the peripheral region, but extend into the mass of sporogenous cells and in some cases ramify entirely through the loculus, occupying more than one-half of the sporangial cavity. The origin of the tapetum was not definitely determined, but it seems highly probable that it arises from the sterilization of sporogenous tissue rather than from the inner cells of the wall, and that all of the sterile cells within the sporangium are of the same ancestry. The tapetal cells vary in size, many of them being as large as the microspore mother cells. They are binucleate and are more vacuolate than are the functional spore mother cells. The two nuclei of a single cell are usually side by side either at the center of the cell or at one end. Each nucleus contains one nucleolus or occasionally more.

CALDWELL (11) describes a condition for *Lemna minor* in some respects similar to that just outlined. He finds that during the early stages of the heterotypic division the cells of the tapetum sometimes divide and form groups of cells which project into the mother cell region; that the number of microspore mother cells is not reduced by the presence of the tapetal cells, although only a comparatively few developed spores, the others disorganizing and aiding the tapetum in nourishing the functional mother cells. In *I. Sultani* only about half the number of microspore mother cells arise that one would expect from the size of the sporangium. As indicated, not all of the tapetal cells arise at the periphery of the sporogenous mass, but many of them originate side by side with the microspore mother cells. The small number of microspore

mother cells may doubtless be related to the probable hybrid nature of the form of *Impatiens Sultani* used. The distinction between the functional and non-functional sporogenous tissue can clearly be seen at an early stage, and still shows distinctly when the spore mother cells are in synapsis. The latter are still angular and are only just beginning to separate (fig. 20).

As is customary at the time of synapsis, the chromatic substance is massed against the nuclear membrane, with the single large vacuolate nucleolus projecting out from one side. As the prophase of the heterotypic division advances and a delicate spirem fills up the nuclear cavity, the cells become almost entirely free and round off, while the tapetal cells still remain somewhat angular in outline and often contain more than the 2 nuclei of the earlier stage (fig. 21). Their nuclei have become granular, lack a nucleolus, and stain more densely than before. In general, the entire mass of cells has separated from the wall. The ovule at this age shows no sign of the inner integument.

As the anther increases in size, the microspore mother cells become entirely rounded off and the spirem takes on a double appearance, whether due to a splitting of a single spirem or an approximation of two was not apparent. At this time the spirem is thicker and less delicate than the spirem immediately following synapsis (figs. 21, 22). The cytoplasm has an obscurely radiate appearance, being densely granular about the nuclear membrane and more vacuolate toward the cell membrane. The spirem thickens, becomes irregular, and segments transversely into bivalent chromosomes. The majority of the segments come to lie against the nuclear membrane and show clearly their double nature in the forms of X's, Y's, and V's. They are rough in outline and are connected here and there by delicate threads (fig. 23), similar to those figured by MOTTIER (33) for *Acer Negundo* and *Staphylea trifolia*. The nucleolus still persists and at this stage there may be two, a large and a small one.

The granular area surrounding the nucleus has become still more marked and closely resembles the kinoplasmic region described by ALLEN (1) for the pollen mother cells of *Larix* and by numerous other writers. The peripheral cytoplasm with its large meshes

draws away from the cell membrane at various points. At this stage cellulose begins to be deposited about the cell and when the chromosomes have reached the equatorial plate a broad cell wall of cellulose is formed (fig. 27). As the chromosomes shorten and thicken, they become smooth in outline and numerous fibers heavier and longer than those mentioned for an earlier stage (fig. 23) appear within the nuclear cavity. These fibers seem to have no apparent relation to the fibers of the kinoplasmic region, although at this time the nuclear membrane has become indistinguishable from the cytoplasm at various places (figs. 24, 25). The fibers are tufted and may extend from a given chromosome across the nuclear cavity to other chromosomes or to the nuclear membrane. At this time no nucleoli are visible within the nuclei and there is the possibility that their substance has assisted in the formation of the fibers.

After the nuclear membrane has entirely disappeared many fibers appear about the chromosomes (fig. 26). They extend beyond what was the original area of the nucleus and doubtless there has been a union of intra- and extra-nuclear fibers in the formation of the multipolar spindle (fig. 26). By the time metaphase is reached the spindle has become sharply bipolar and extends across the entire cell (fig. 27). The cytoplasm surrounding the spindle has lost the dense granular appearance of the early prophase stages and stains less densely than does the peripheral region.

While I am not willing to make an unqualified statement regarding the number of bivalent chromosomes, it seems most probable from the study of the heterotypic divisions in the megaspore and microspore mother cells that the haploid number is 7, as I have been unable to count more than that number. No stages in microsporogenesis were obtained between metaphase of the heterotypic division and the tetrads following the homotypic division.

When the tetrads are formed the microspores are surrounded by the very thick cellulose wall of the mother cell. Each microspore is a little over 3 times longer than wide and possesses a reticulated membrane. At this time its nucleus is not spherical,

but simulates the outline of the cell and its chromatic material is distributed unevenly throughout the nuclear cavity. Several large masses of chromatin are mingled with chromatic threads which extend out from them in various directions (figs. 28, 29).

The loculi containing these tetrads also contain densely staining tapetal cells. These cells still have large vacuoles, but the cytoplasm stains more densely than in earlier stages and their nuclei contain one nucleolus each. Outside the tapetum is the flattened layer of cells, and beyond this the remainder of the wall is still undifferentiated.

Later, when the microspores have broken away from the old mother wall, the endothecium with its spirally thickened cell walls forms just beyond the flattened layer. The tapetal cells, in general, are still in good condition, some of them centrally located having increased very greatly in size and number of nuclei. Compare the tapetal cell (fig. 33) which was magnified 810 times with the microspore (fig. 30) which was taken from a loculus of the same age and magnified 1620 times. The number of nuclei in these tapetal cells may reach as high as 11 or more. These unusually large cells show stages in disintegration, and it is difficult to find one which has not begun to break down. A large number of nuclei, ranging from 6–13 in the tapetal cells of *Hepatica acutiloba*, has been reported by COULTER (**14**). SCHAFFNER (**39**) in his description of *Typha latifolia* states that the tapetal cells increase greatly in size while the tetrads are forming, but speaks of but 2 nuclei being formed in each cell.

When the microspores escape from the tetrad the chromatin of their nuclei consists of heavy, anastomosing strands which soon give rise to several distinct masses of chromatin connected with each other by more or less delicate threads. In by far the greater number of cases, if not always, these masses correspond in number with the haploid number of chromosomes (fig. 30). No nucleolus is visible at this time. There is evidently no true spirem formed in the division of the nucleus to form the generative and tube cells, but the rather imperfect reticulum of the very young microspores gives rise directly to the chromosomes at a considerable time before the organization of the spindle. It is a very common occurrence

to find all the microspores of an anther in an apparently resting stage and showing distinctly 7 chromatic masses.

The microspore divides and forms a more or less vacuolate 2-celled pollen grain (figs. 31, 32). The tube nucleus is normally spherical and lies more or less near the center of the developing pollen grain (figs. 32, 34, 35). The generative cell occupies various positions within the cytoplasm of the tube cell, and at all times its nucleus is smaller and its reticulum is much less delicate than that of the tube nucleus. The pollen grain grows and its cytoplasm becomes densely filled with food granules. At this time the generative cell may either be attached to the wall of the pollen grain or lie free in the cytoplasm (figs. 34, 35).

When the anther is ready to dehisce, it is impossible to distinguish the cytoplasm of the generative cell, and its nucleus has changed from nearly spherical to a very slender lunate form (fig. 36). At first it was thought to be a sperm nucleus, but while these crescent-shaped nuclei are very characteristic of the developing male gametophyte, no more than one to each pollen grain was ever found. When the nucleus is in this condition it contains several chromatic masses in the center and stains a diffuse yellow at either end. In all cases where the nucleus could be seen clearly throughout its entire length 7 chromatic masses were visible (fig. 36). The mature pollen grains, in longitudinal section, present an almost rectangular appearance and possess 4 germ pores, one at each corner. No instances of the division of the generative cell while still within the anther were discovered, and it is doubtful whether this division takes place until some time after pollination.

Ovule after pollination

The pollen tube enters the embryo sac after the chalazal haustorium has developed. Many of the embryo sacs of a given ovary were found containing the pollen tube contents in their micropylar region. While no experiments were made to eliminate all chance of cross-pollination, the conditions under which these plants were grown in the greenhouse render it very probable that many of the flowers were self-pollinated. The pollen tube enters the embryo sac at one side of the filiform apparatus and either

continues down the same side of the sac near to the region of the egg nucleus or crosses over the synergid and extends down the other side (figs. 37, 38). After this has occurred it is difficult to find both of the synergid nuclei. Doubtless one of them soon becomes disorganized, due to the effect of the presence of the pollen tube. SMITH (40) describes the pollen tube of *Eriocaulon* as either passing through a synergid or between the two without destroying them.

In *I. Sultani* the tube nucleus was usually visible in the embryo sac, but it was often difficult to discover the sperms, due to their small size and also to the presence of many small densely staining bodies which often suggested parts of nuclei but were possibly food particles. The sperms are coiled or spiral in outline as they approach the egg and polar nuclei. In fig. 38 the two sperms are both near the egg nucleus, one is directly over the latter and the other is at its side, still in the dense strand of cytoplasm which marks the path of the pollen tube contents, and doubtless is on its way to the two polar nuclei. No sperm cytoplasm is visible and the nucleus is a spiral body made up of dark and light areas, the former of which are doubtless masses of chromatin. The character of the sperm shown in fig. 39 differs somewhat from those in the preceding figure. Here a sperm nucleus is situated one at either side of the egg nucleus; the one at the right is coiled tightly and shows no distinction between chromatic and clear areas, but stains a clear light blue. It was doubtless on its way through the cytoplasm at the side of the egg to the endosperm nucleus lying directly below the egg.

No stages in the actual fusion of the egg and sperm were seen. The fertilized egg differs so slightly from the unfertilized one that it is difficult to decide in a given case whether or not fertilization has occurred. In general, however, the fertilized egg increases slightly in size and its limiting membrane is more conspicuous than it is in earlier stages (fig. 40). Figs. 38 and 40 have the same magnification and the increase in size is evident.

It seems probable that the polar nuclei unite at an early stage in the fusion of the sexual nuclei. The nuclear membranes of the two polars break down where they come in contact and one of the nucleoli passes over into the other nucleus (figs. 41, 42). Both

nucleoli possess one or more vacuoles. What appears to be a later stage in the fusion of the two polars is given in fig. 43. A dense granular mass, the entering nucleolus, seems to be in vital contact with the nucleolus of the receiving nucleus and gives the impression of giving of its substance to help in the formation of the nucleolus of the resulting endosperm nucleus. The characteristically large vacuole of the primary endosperm nucleolus has already appeared. Not all of the entering nucleolus fuses with the receiving nucleolus, however, for coarse strands radiate out from the dense mass of nucleolar substance and appear to be adding to the reticulum of the nucleoplasm. A similar radiating mass has been observed in one of two polars. In this case it might represent a stage in the fusion of the second sperm with one of the polars before the two polar nuclei had united. Similar masses have also been seen in the megaspore mother cell, and here also the nucleolus doubtless contributes to the chromatic substance.

The fusion of the two polars has been figured by numerous writers for many different plants. In *Nicotiana Tabacum* (GUIGNARD **23**) the two nucleoli remain distinct in the fusion nucleus for some time before fusing. VANDENDRIES (**44**) figures for *Cardamine pratensis* two nucleoli within the primary endosperm nucleus with a sperm against one side of it. He says that when the pollen tube enters the cavity of the embryo sac the two polar nuclei have begun to fuse but the nucleoli are still distinct. In *I. Sultani*, however, the fusion of the two polar nuclei begins relatively much later and takes place very quickly. In describing the fusion of the two polars of *Arisaema triphyllum*, GOW (**18**) says that the fusion endosperm nucleus frequently contains two nucleoli.

It seems highly probable that after the primary endosperm nucleus is formed the second sperm unites with it. By this time the sperm nucleus appears to be larger than it was in earlier stages. In fig. 44 it is just at the point of piercing the nuclear membrane, and in fig. 45 it is within the primary endosperm nucleus and lying either above its nucleolus or within it. It was impossible to determine if the second sperm, in all cases, waited until the primary endosperm nucleus was formed before becoming functional. GUIGNARD (**23**) is convinced that in the Malvaceae the time of

formation of the secondary nucleus is constant for a given genus. In *Lavatera* and others it is formed before fertilization, while it is formed after in *Hibiscus*.

Following fertilization a micropylar haustorium is formed. The primary endosperm nucleus divides before the division of the fertilized egg. After a few divisions have taken place several of the resulting endosperm nuclei pass up through the micropylar part of the embryo sac (figs. 46, 47) out into the micropyle and form a haustorium which emerges from the micropyle and crosses over the space between the latter and the funiculus (figs. 49*a*, *b*). As the haustorium encounters the funiculus it either extends along the funiculus some little distance before entering it or penetrates it immediately and branches freely within its tissue (fig. 53).

In the early stages, as the endosperm nuclei pass through the upper part of the sac, they are surrounded by cytoplasm rendered dense by the presence of a large amount of food substance and consequently the nuclear membrane is entirely obscured (figs. 46, 47). The densely staining filiform apparatus, all that remains of the two synergids, is still present, but it is more widely separated from the enlarged part of the embryo sac than in earlier stages (fig. 47). The narrow micropylar part of the sac where the synergids of the mature embryo sac were situated has widened and encroached upon the small disorganizing cells of the inner integument. These cells have now disappeared except for a few remains and large regular cells limit the micropylar cavity into which the sac has pushed (cf. figs. 9, 14, 47). At this stage the fertilized egg is still undivided and several endosperm nuclei lie below as well as above it. These nuclei are not shown in fig. 47, as they occurred in a different section from the one sketched.

In the later stages in the development of the micropylar haustorium but few nuclei are present in it. These are very large and contain a large nucleolus and stain bright red with safranin (fig. 53). This haustorium was seen to persist up through the oldest stages studied, namely, those containing embryos with radicle and cotyledons differentiated.

The micropylar haustorium of *I. Sultani* differs from that of *I. amphorata*, as described by LONGO (**28**), in not entering the

outer integument. It simply pierces the funiculus and branches extensively within it.

As in *I. amphorata* (LONGO **28**), *I. Sultani* possesses a chalazal haustorium as well as a micropylar one. This haustorium is much less extensive than is the micropylar one. One of the endosperm nuclei at the antipodal region becomes very large, and with its surrounding cytoplasm forms a long cell which pierces through the sac and one end of it enters the chalazal tissue, while the other end remains in contact with numerous normal endosperm cells (figs. 50, 51, 53).

It was difficult to secure a vertical section through this haustorium, as a series of sections which cut through the embryo vertically would section the haustorium somewhat diagonally. Fig. 50 shows the outline of the cell, but no nucleus, while fig. 51 shows the embryo sac portion with a large nucleus, but the chalazal part was cut so that all connection between chalazal tissue and haustorium was lost. This large haustorial cell contains a densely granular cytoplasm and is doubtless active in conveying nutriment from the chalaza to the endosperm. This haustorium does not remain active as long as the micropylar one. By the time the cotyledons of the embryo have become differentiated it is not so prominent as in earlier stages, while the micropylar haustorium still seems very active (fig. 53).

The endosperm develops more rapidly at the micropylar and chalazal regions than at the sides of the sac. A layer of cytoplasm with a single row of free nuclei persists at the sides for some time, while at the poles of the sac walls come in early to separate the nuclei (figs. 49*a*, 50, 51). With the presence of two rows of nuclei at the sides, walls form about the outer layer of nuclei, while those of the inner layer remain free (fig. 48) until some time later, when they are separated by walls, and the endosperm is composed entirely of cells (fig. 53). The size and shape of the embryo sac have undergone marked changes during endosperm formation. At the time of fertilization the outline of the sac is similar to that shown in fig. 54, with the early antipodal haustorium opposite the micropylar part of the sac. Later, during early endosperm formation, the sac elongates and widens slightly at the micropylar region. Below

this it enlarges considerably on the side away from the raphe, and the sac becomes asymmetrical (fig. 55). This lateral growth continues until it extends even beyond the original position of the antipodal haustorium, with the result that the chalazal haustorium of endosperm origin comes to lie at the side of the sac rather than at its base, and the embryo sac extends below the chalaza (fig. 53).

The embryo develops less quickly than does the endosperm. As stated earlier, the fertilized egg does not divide until after many free endosperm nuclei have been formed. The proembryo becomes differentiated into suspensor and embryo early in its development. By the time the embryo consists of several cells the suspensor, in a longitudinal section, shows but two cells. The cell adjoining the embryo is broader than long and the terminal one is but slightly longer than wide (fig. 49*a*). The suspensor, doubtless on account of the very effective micropylar haustorium, appears to be but a short-lived organ. It neither elongates nor becomes bladder-like, as is the case for many of the angiosperms, but soon breaks down and disappears. It shows signs of disintegration before the cotyledons of the embryo appear (fig. 52), and by the time they are differentiated the suspensor has disappeared. The embryo develops at the tip of the suspensor and by the time the endosperm consists of two layers of cells about the periphery of the embryo sac the radicle and two cotyledons have become differentiated (figs. 53, 56).

The embryo and the chalazal haustorium do not occur in the same vertical plane, therefore it is impossible to secure satisfactory sections of the two from the same embryo sac. In the oldest stage studied a band of endosperm cells lines the sac (figs. 53, 56). The endosperm lies in close contact with the axis of the embryo and the sides of the cotyledons, but it is separated from the chalazal end of the embryo by a large cavity. Unfortunately, through lack of study of the seeds of *I. Sultani*, I was unable to determine the fate of the endosperm. According to GUIGNARD (**22**), a thin layer of endosperm remains undigested in the mature seed. BRUNOTTE (**10**), from his study of the Balsaminaceae, believes that the descriptions of the systematists for the mature seed should be changed.

Instead of describing the seed as having no endosperm, he would say that there is a small amount of endosperm present.

Summary

1. The ovule possesses but one hypodermal archesporial cell.

2. The archesporial cell is also the megaspore mother cell.

3. An axial row of two cells is formed. The chalazal cell is the mother of the embryo sac.

4. A normal 8-nucleate sac is formed.

5. There is a variation in the position of the synergid nuclei, due to their age.

6. The two polar nuclei come in contact directly beneath the egg and do not fuse until after the pollen tube has entered the embryo sac.

7. The 3 antipodals may be either 3 cells or a group of 3 nuclei cut off from the upper region of the sac by a membrane.

8. The antipodals disappear soon after the egg apparatus is formed.

9. The megaspore mother cell and the early 2-nucleate embryo sac are bounded at the apex and sides by the nucellar epidermis.

10. The embryo sac absorbs the nucellar epidermis and by means of an antipodal haustorium absorbs all of the nucellus between the sac and the chalaza.

11. The tapetum is derived from the inner layer of the inner integument.

12. The outer integument arises from the inner integument.

13. Binucleate tapetal cells surround the microspore mother cells. They also extend into the mass of sporogenous cells and separate the functional mother cells into groups.

14. The nucleus of the generative cell of the pollen grain apparently does not divide before pollination.

15. The pollen tube enters the embryo sac along the side of the filiform apparatus and extends down one side of the embryo sac until it is near the egg nucleus.

16. Two coiled sperm nuclei are often seen near the egg nucleus.

17. It seems very probable that triple fusion occurs.

18. An extensive micropylar haustorium and a more simple chalazal one develop from the endosperm.

19. The embryo possesses a short suspensor.

20. The bivalent chromosomes in both megasporogenesis and microsporogenesis show X's, Y's, and V's.

21. A multipolar spindle appears in the prophase of the heterotypic division in microsporogenesis.

22. The nucleus of the microspore has but a short period of rest; the prophase of division is initiated early and persists for some time.

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EXPLANATION OF PLATES XIV, XV

All figures were drawn with the aid of an Abbé camera lucida and are reduced one-half in reproduction. The number accompanying the description of each figure indicates the magnification before the reduction. The lettering of the figures is as follows: *ii*, inner integument; *oi*, outer integument; *mc*, megaspore mother cell; *n*, nucleolus; *f*, funiculus; *ma*, micropylar cell of axial row; *e*, epidermis of nucellus; *t*, tapetum; *s*, stringy cells of the nucellus; *en*, egg nucleus; *sn*, synergid nucleus; *cv*, central vacuole; *p*, polar nucleus; *mm*, microspore mother cell; *dn*, disintegrating nuclei; *tn*, tube nucleus; *gn*, generative nucleus; s^1, sperm nucleus; s^2, sperm nucleus; *fa*, filiform apparatus; *ptc*, pollen tube contents; *rp*, receiving polar; *m*, micropyle; *ah*, antipodal haustorium; *mh*, micropylar haustorium; *ch*, chalazal haustorium; *sp*, suspensor; *c*, chalaza; *ed*, endosperm; *vs*, vascular strand; *r*, radicle; *co*, cotyledon; *w*, wall; *pe*, primary endosperm nucleus; *ra*, raphe; *cu*, cells with cutinized walls; *nrp*, nucleolus of receiving polar; *edn*, endosperm nuclei.

PLATE XIV

Fig. 1.—Vertical section of ovule before integuments have appeared; ×828.

Fig. 2.—Vertical section of ovule showing origin of inner integument and large megaspore mother cell; ×810.

Fig. 3.—Vertical section of ovule slightly older than fig. 2; ×810.

Fig. 4.—Vertical section of ovule with nucleus of megaspore mother cell in synapsis; ×810.

Fig. 5.—Vertical section of megaspore mother cell with nucleus in second contraction stage of prophase of heterotypic division; ×1620.

Fig. 6.—Vertical section of ovule showing origin of outer integument and segmented spirem of megaspore mother cell; ×500.

Fig. 7.—Vertical section of megaspore mother cell showing tetrad formation in nucleus; ×1300.

Fig. 8.—Vertical section of nucellus after 2-celled axial row has been formed; ×1300.

Fig. 9.—Vertical section of portion of ovule containing 2-nucleate embryo sac; ×1000.

Fig. 10.—Vertical section of 2-nucleate embryo sac with surrounding nucellus and tapetum; nuclei of embryo sac in prophase of division; ×810.

Fig. 11.—Vertical section of young 4-nucleate embryo sac; combination of 3 serial sections; ×810.

Fig. 12.—Vertical section of slightly older sac with nucellus and disintegrating epidermis; ×810.

Fig. 13.—Vertical section of still older 4-nucleate embryo sac with basal portion of epidermis still intact; ×1000.

Fig. 14.—Vertical section of early 8-nucleate embryo sac with nucellus at base and tapetum at either side; ×1000.

Fig. 15.—Vertical section of early stage in formation of egg apparatus: synergid nuclei each above a large vacuole; ×1000.

Fig. 16.—Vertical section of micropylar region of embryo sac showing 2 synergids; synergid nuclei have reached center of the 2 synergid cells; ×1000.

Fig. 17.—Vertical section of 8-nucleate embryo sac before the 2 polar nuclei have reached their position directly beneath egg; combination of 2 serial sections; ×1000.

Fig. 18.—Vertical section of antipodal region of 8-nucleate sac before antipodal polar has moved toward micropylar polar; the 3 antipodals show as distinct cells; combination of 2 serial sections; ×1620.

Fig. 19.—Vertical section of embryo sac after antipodals have disappeared and antipodal haustorium has begun to develop; micropylar tip of sac was covered by inner integument; ×1000.

Fig. 20.—Cross-section of microsporangium while spore mother cells are in synaptic stage; ×500.

FIG. 21.—Cross-section of contents of microsporangium soon after chromatic substance of microspore mother cells has formed a spirem following synapsis; ×500.

FIG. 22.—Section of microspore mother cell slightly older than those in preceding figure; nucleus contains spirem showing its double nature; ×1620.

FIG. 23.—Section of microspore mother cell soon after spirem has segmented; 2 nucleoli present, small one directly over large one was omitted from sketch; ×1620.

FIGS. 24, 25.—Sections of 2 microspore mother cells after bivalent chromosomes have shortened and become smooth in outline and intranuclear fibers have appeared; in fig. 25 a thick wall is beginning to form about the mother cell; ×1620.

FIG. 26.—Section of microspore mother cell with multipolar polyarch spindle; heterotypic division; ×1750.

FIG. 27.—Section of microspore mother cell showing bipolar spindle of heterotypic division; bivalent chromosomes arranged at equatorial plate; ×1620.

FIG. 28.—Cross-section of tetrad; ×1620.

FIG. 29.—Vertical section of tetrad with but 2 of the microspores visible; ×1620.

FIG. 30.—Vertical section of young microspore; nucleus has passed through a very short resting stage and has entered upon a prolonged prophase; ×1620.

FIG. 31.—Cross-section of young pollen grain; large central vacuole present and tube and generative nuclei at one side of pollen grain; ×1620.

FIG. 32.—Vertical section of slightly older pollen grain than fig. 31; generative cell lies near center of pollen grain; ×1620.

PLATE XV

FIG. 33.—Section of one of large multinucleate tapetal cells which occur within microsporangium after microspores have separated from tetrads; nuclei in various stages of disintegration; ×810.

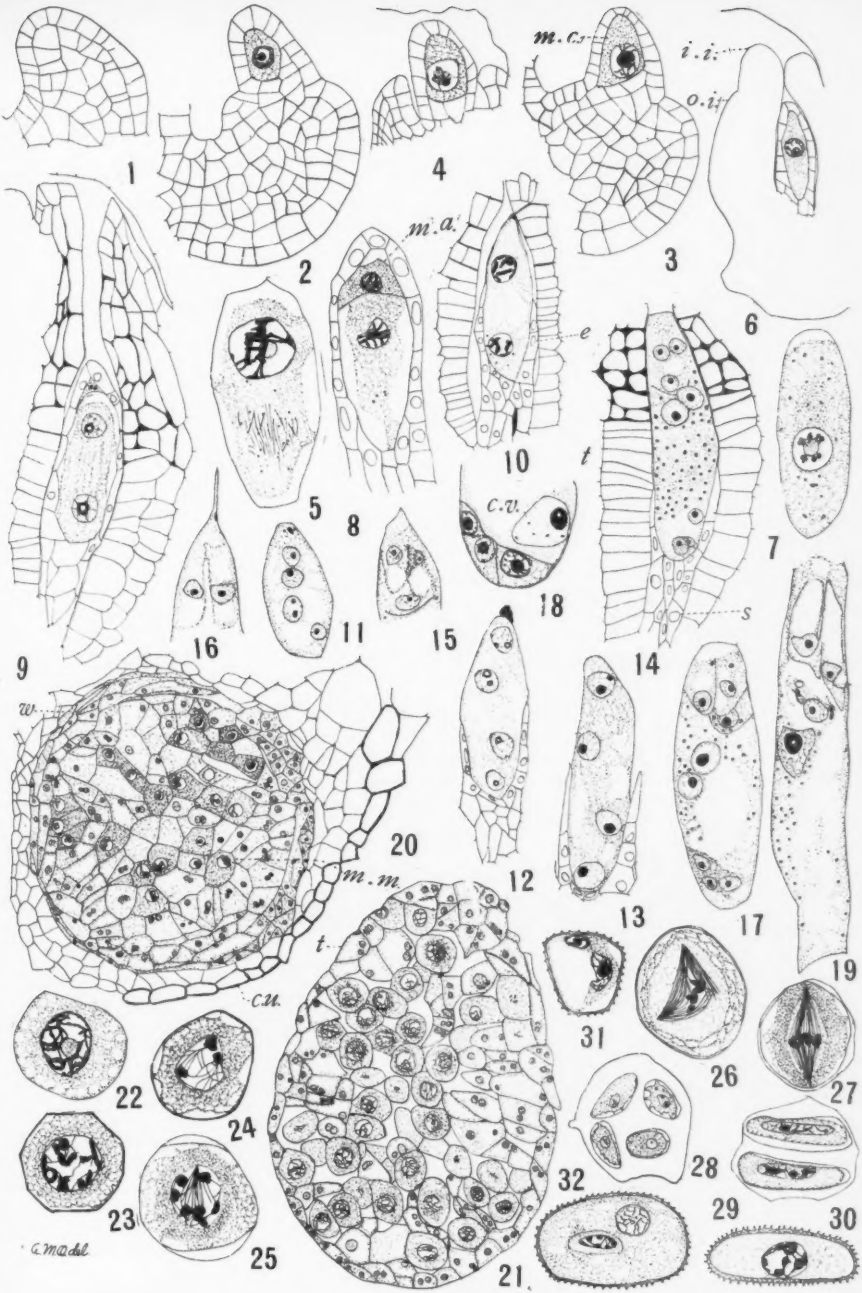
FIGS. 34, 35.—Vertical sections of nearly mature pollen grains; note change in size and cytoplasmic contents from fig. 32; cytoplasm packed full with food which is doubtless starch grains; in fig. 34 generative cell lies against wall of pollen grain, while in fig. 35 it lies free within cytoplasm of tube cell; ×1620.

FIG. 36.—Cross-section of mature pollen grain; cytoplasm of generative cell cannot be distinguished from that of tube cell; generative nucleus forms a crescent and contains 7 distinct chromatic masses; ×1375.

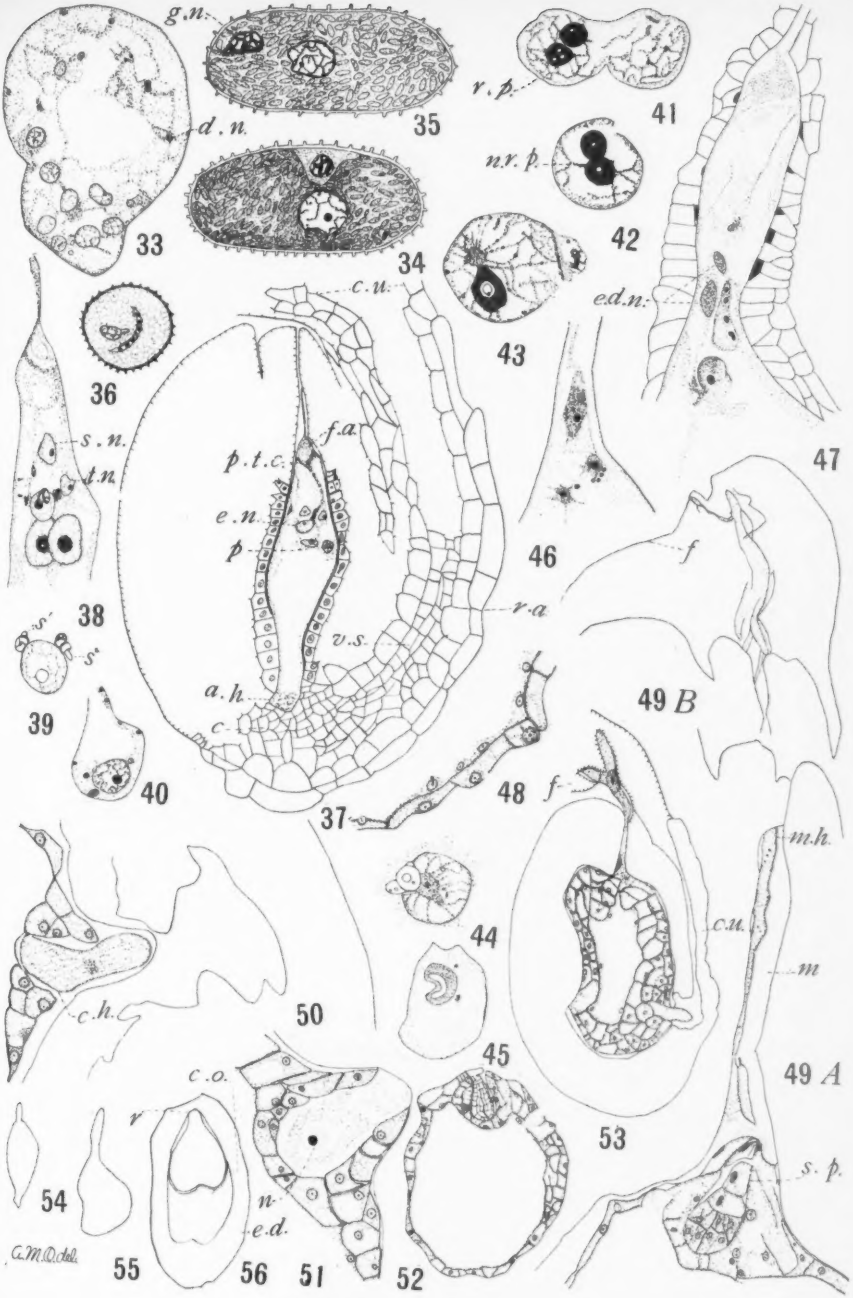
FIG. 37.—Vertical section of ovule after pollen tube has entered embryo sac; sketch is largely in outline and was derived from 3 serial sections; ×500.

FIG. 38.—Vertical section of micropylar region of embryo sac after pollen tube has entered sac; ×1000.

FIG. 39.—Two sperms near egg nucleus; ×1620.



OTTLEY on IMPATIENS



OTTLEY on IMPATIENS

FIG. 40.—Fertilized egg; ×1000.

FIGS. 41–43.—Stages in fusion of the 2 polar nuclei; ×1620.

FIGS. 44, 45.—Stages in fusion of second sperm nucleus with endosperm nucleus; fig. 44, ×1620; fig. 45, ×1625.

FIG. 46.—Vertical section of apex of embryo sac showing 3 endosperm nuclei on their way to form micropylar haustorium; another section shows endosperm nucleus below original position of primary endosperm nucleus; ×500.

FIG. 47.—Vertical section of micropylar portion of embryo sac after primary endosperm nucleus has divided several times; sac has enlarged beneath filiform apparatus; ×1000.

FIG. 48.—Portion of endosperm present at one side of embryo sac after embryo has formed; ×500.

FIG. 49*a*, *b*.—*a*, vertical section through micropyle with micropylar haustorium, and through embryo sac at base of micropyle; young embryo with short suspensor surrounded by endosperm cells; ×500; *b*, vertical section of micropylar haustorium as it extends across space from micropyle to funiculus; *a* and *b* are sketches of same haustorium, but taken from different sections; ×500.

FIG. 50.—Section through chalazal portion of ovule; chalazal haustorium and endosperm cells are filled in while only outline of chalazal tissue is given; sketch is from same ovule as fig. 49*a*, and is a combination of 2 sections; ×500.

FIG. 51.—Vertical section of chalazal haustorium with surrounding endosperm cells; haustorium cut somewhat diagonally; ×500.

FIG. 52.—Vertical section through embryo sac after a many-celled embryo has developed; endosperm at base and at one side consists of but one layer of cells, at the other side consists of several layers, and in another section of this same embryo sac chalazal haustorium occurs in this thickened portion of endosperm; ×162.

FIG. 53.—Outline sketch of vertical section of ovule containing embryo of 2 cotyledons; embryo does not show in section; combination of 2 sections; ×162.

FIG. 54.—Outline sketch of vertical section of embryo sac at time of fertilization or slightly later; growth has taken place at antipodal and at median regions; ×162.

FIG. 55.—Outline sketch of vertical section of embryo sac after embryo has been developed; narrow micropylar portion of sac has lengthened and increased somewhat in width; side opposite raphe has pushed out into integument, giving an asymmetrical sac; ×162.

FIG. 56.—Outline sketch of vertical section of embryo and accompanying endosperm tissue; embryo is differentiated into radicle, hypocotyl, and 2 cotyledons; ×162.

NOTES ON AMERICAN WILLOWS

II. THE SPECIES RELATED TO *SALIX GLAUCA* L.

CAMILLO SCHNEIDER

In my first paper[1] I dealt with *Salix arctica* Pall. and its relatives. These species are mostly united with *S. glauca* L. and its congeners in one group or section by such American salicologists as P. A. RYDBERG and C. R. BALL. European students of willows like N. J. ANDERSSON, A. and E.-G. CAMUS, and O. v. SEEMEN referred the two species to different sections, and I have always thought it best to regard each species as a representative of a distinct group. It is not an easy task to draw a line between the forms of the GLAUCAE on the one hand and those of the *arctica* group on the other, but this is true of most of the sections in a genus like *Salix*, where it is difficult to define groups of closely related species. As I have already explained in SARGENT, Pl. Wils. **3**:136. 1916, the name ARCTICAE is not available to designate the group of which *S. arctica* Pall. is the type, because it was first used by ANDERSSON (1858) for a section containing *S. Hookeriana* Barr., *S. speciosa* Hook. and Arn., non Host. (*S. alaxensis* Cov.), etc., which in 1868 ANDERSSON included in his sect. NIVEAE B. VILLOSAE; therefore I (*l.c.* 140) proposed the name DIPLODICTYAE for this group, but at this time I also kept the OVALIFOLIAE of RYDBERG as a separate unit, expressing, however, a doubt "whether the species united by RYDBERG in this section really belong in the same group." At present I believe that *S. ovalifolia* should be placed in the same section with *S. arctica*, and consequently the name OVALIFOLIAE must be adopted for this group. To distinguish between those two sections the color and pubescence of the bracts (or scales) seems to afford a rather reliable character. In the OVALIFOLIAE the bracts are usually more or less bicolor, being pale at base and dark brown, fuscous, or even blackish toward the apex, while the forms of the GLAUCAE mostly have uniformly yellowish, light brown, or straw-colored bracts, which sometimes (especially in the upper part of

[1] BOT. GAZ. 117–142. 1918.

the ament) are reddish or purplish toward the apex, but never become really fuscous or blackish. Furthermore, the pubescence of the 2 kinds of bracts is of a different character. In the first group it usually consists of rather long, straight, silky hairs, of which at least the uppermost are about the same length as the bract, which mostly does not bear many short hairs on its surface, and often becomes nearly glabrous. In the second group the hairs are comparatively shorter, less straight, and rarely distinctly silky, but are softer and sometimes a little curly. As a whole the bracts are more or less covered with pubescence, and are rarely distinctly ciliated at apex with long silky hairs. These characters are usually more easily detected in the female than in the male specimens, which are often more similar in the two groups. It takes some time for the student to become familiar with these peculiarities, which are by no means clearly recognizable in every specimen. There are of course exceptions also, but in such cases we find other characters to determine the real affinity of a certain form. Many so-called intermediate forms are of hybrid origin, or should receive closer observation in the field before defining their taxonomic position. This is what I have to say at present regarding the separation of the sections GLAUCAE and OVALIFOLIAE. Later I hope to have the opportunity to discuss in detail the systematic arrangement of the American species of *Salix*.

As I now understand them, the following species belong to the section GLAUCAE: *S. anamesa* Schn., *S. brachycarpa* Nutt., *S. chlorolepis* Fern., *S. cordifolia* Pursh, *S. desertorum* Rich., *S. fullertonensis* Schn., *S. glauca* L., *S. lingulata* And., *S. niphoclada* Rydbg., and *S. pseudolapponum* v. Seem. I do not include in this group *S. chlorophylla* And., *S. McCalliana* Row., *S. Nelsonii* Ball, *S. saskatchavana* v. Seem., and *S. idahoensis* (Ball) Rydbg., which RYDBERG places in his section ARCTICAE (Fl. Rocky Mts. 190. 1917), which seems to me an unnatural mixture of species of different affinities.

1. S. GLAUCA L., Sp. Pl. **2**:1019. 1753.—Before we can decide whether any American forms or which of them are to be referred to this species it seems necessary to discuss the characters of the typical *S. glauca* L. It is founded on "363. *Salix* foliis integris subtus tenuissime villosis ovatis. Tab. VIII. fig. p. and Tab. VII.

fig. 5" in LINNAEUS' Fl. Lapp. 290. 1737. The description and figure given by the author in this place give a rather good idea of his type. Furthermore, ENANDER (Stud. Salic. Linnés Herb. pp. 51, 54, 59. 1917) describes the female and male specimens of *S. glauca* genuina, typica or vera in Linnaeus' herbarium. Following LINNAEUS and ENANDER, I find the following characters of what has to be called the typical *S. glauca:* Frutex bi- vel tripedalis. Rami rubescentes, glabri; ramuli novelli villosi. Folia ovata, lanceolata, ovali-lanceolata vel ovato-oblonga, utrinque fere aequaliter attenuata vel inferiora apice obtusa, superiora magis oblonga acutiora, integerrima, 15:8 vel 40:12 ad 60:15 vel 55:20 mm. magna, utrinque (subtus tamen densius) villosi vel superne pilis parcius obsita vel fere glabra, non vero nitida, subtus pallidiora, "villis oblongis raris hirsuta" vel "pilis albicantibus vestita"; petioli 8–10 mm. longi, villosi; amenta pedunculis ad 3 cm. longis foliolis circ. 4 ceteris similibus instructis suffulta; flores masculi bracteis pallidis pilosis, filamentis basi pilis crispatis ornatis antheris testacei coloris instructis; feminei bracteis similibus, ovariis capsulisve tomentosis sessilibus, stigmatibus stylisque quasi semipalmato-alcicornibus.

Not having sufficient herbarium material from Lapland at my disposal, I think it best to add the following characters given by ANDERSSON in his Salic. Lap. 73, *fig. 21.* 1845:

> Amenta serotina ramulos breves crassiusculos tomentosos foliis ceteris vix minoribus 3–6 vestitos terminantia, iisque plerumque longiora, cylindrica, obtusa, erecta, demum sublaxa; mascula 1–2 uncialia, densa, squamis oblongis, obtusis, fulvis apice roseis, pilis albis longis rectis villosissimis, stam. 2, filamentis fulvis, basi barbatis, antheris globosis prius coerulescenti-roseis; feminea subdensiflora, abrupta, obtusa, 1–3 uncialia, primum rigida, demum laxa, squamis fulvis apice roseis, oblongis, obtusis, ventrem capsulae superantibus, albo-villosis; capsulae pedicello nectario lato quadrangulari pl.m. profunde partito, dimidio breviori, brevissime pedicellatae, ovales vel conicae, obtusae, lana alba densissime tomentosae, stylis aut omnino geminis aut fere usque ad basin bipartitis (ut eorum pars, quando adest, semper sub lana capsulae lateat), stigmatibusque linearibus divaricato-bipartitis, rufo-fulvis terminatae.

Judging by these characters we have to decide, I believe, whether there are in America forms identical or closely related to the typical

S. glauca from Northern Europe. According to the leading European salicologists *S. glauca* is rather variable, but I fail to find a good arrangement of the different variations already known from Europe and Northern Asia in the existing literature. It is impossible to judge the American forms correctly without having a clear understanding of the Asiatic forms already described, because it is to be expected that the forms from Eastern Asia will have the closest affinity with the American forms.

No mention is made of *S. glauca* by PURSH (1814) or MICHAUX (1820), or even by HOOKER (1839). It was ANDERSSON who in 1858 first mentioned *S. glauca* as occurring "in provinciis septentrionalibus et arcticis Americae borealis." He further said:

> Haec species . . . . in arcticis regionibus Americae habitu externo vix nostrae similis exstat. Specimina tamen a Seemann in parte occidentali et a Lyall in Disco Island lecta, nec non e "Rocky Mountains" reportata cum nostris tamen ita congruunt, ut de identitate non dubitare liceat. Folia nunc utrinque molliter villosa et incana, nunc denudata subviridia, amenta semper foliato-pedunculata, capsulae brevius pedicellatae. Huic certissime ut forma tantum associanda—*villosa*. *S. villosa* (D. Don) Hook. *l.c.* p. 144, no. 3.

This *S. villosa* Barratt apud HOOKER has to be ascertained before anything else can be done to determine which forms may be referable to *S. glauca*. HOOKER (Fl. Bor.-Am. **2**:145. 1839) said: "that Dr. BARRATT considers it to be the same as *S. villosa* of D. Don, in Pursh, Herb. Canad." I have never seen specimens from a "Herb. Canad." of PURSH, nor do I know whether PURSH ever distributed such a collection.[2] Neither he nor D. DON published a *S. villosa;* there are, however, two species bearing this name, one of SCHLEICHER (Cat. Pl. Helv. ed. 3. 26. 1815) which is a nomen nudum and was probably first mentioned in the first edition of the Catalogue in 1809; the other of FORBES (Salict. Wob. 183. *pl. 92.* 1829) representing a sterile specimen of unknown origin. Thus the

[2] There is, however, a specimen, consisting of 3 leaves only, in herb. N. labeled "*Salix leucodendron* D. Don, in Pursh's Canadian Herb. (collected in Lord Selkirk's Exped. from Mr. Lambert's Herb.)." DON did not publish a species *S. leucodendron*, and I am not yet sure to which species these 3 leaves belong. PURSH'S herbarium was in possession of LAMBERT (see Gard. Chron. 1842, p. 439), but PURSH himself did not collect in Canada at all (see HARSHBERGER, Bot. Philad. 115. 1899). I have not been able to get any information on "Lord Selkirk's Exped."

name *S. villosa* Barr. cannot be used even if the form described by HOOKER under this name could be recognized as a good species. I have been fortunate in seeing photographs and fragments of the types of *S. villosa* preserved at Kew, and also the corresponding specimens of BARRATT's collection in herb. N., and I am convinced that HOOKER included different forms under his *S. villosa*. At first glance his diagnosis fits well the forms described by RYDBERG as *S. Seemannii* (see later) and the material before me from the Yukon Territory, but the character given by HOOKER in the following phrase: "rami foliisque junioribus lana arachnoidea villosis" seems peculiar to me. I cannot detect traces of a "lana arachnoidea" on the specimens before me, and furthermore, the specimen collected by DRUMMOND (no. 7. Herb. H. and B.) which is regarded as the "type" is not characterized by "foliis lato-lanceolatis." There is, however, a specimen in Herb. Torrey (N.) labeled "no. 6. Herb. H.B. and T." and "an *S. villosa* D. Don" in which the lower surfaces of the lanceolate leaves are covered when young with a "lana arachnoidea," the prominent rib being nearly glabrous, while the lateral nerves are almost hidden by the pubescence. Later the leaves become more or less glabrous, and the first or lowermost leaves show nothing but a few scattered long silky hairs. The petioles are nearly glabrous, and the stipules are very small, hardly a fourth of the length of the petiole, very glabrescent, semiovate, and denticulate. This does not agree with HOOKER's statement: "stipulis semicordatis petiolo sublongioribus," which is the case in no. 7; and HOOKER's diagnosis seems to me only explicable if we presume that he mixed two different forms. On the same sheet with no. 6 is also an old fruiting catkin with a leafy peduncle which is identical with those of no. 7. I am not yet sure to what species the sterile branch of no. 6 really belongs.

HOOKER also described a var. "*β. acutifolia;* foliis magis acutis vel subacuminatis," collected by RICHARDSON at Fort Franklin on the Mackenzie River, of which a photograph of the type "no. 76. Hb. H.B. and T." is before me. It consists of 3 pieces of young female flowering branchlets. I also saw a sheet with the label "no. 58. Hb. H. B. & T." ex herb. Torrey (N.) marked "Fort Franklin, Richardson," which contains 2 fruiting and 1 sterile

branchlet of var. *acutifolia* named by RYDBERG *S. villosa* and marked no. 2. Besides these there are 2 sterile branchlets which may belong to var. *glabrescens;* the upper middle one was referred by RYDBERG to *S. villosa*, while the small one at the left corner of the lower label is without number. Furthermore, there are 3 sterile branchlets numbered 1 and named *S. chlorophylla* by RYDBERG which indeed look very much like this species or may be referable to *S. pulchra* Cham. All the specimens are referred (by BARRATT?) to *S. planifolia* Pursh, a very uncertain species which may be identical with *S. chlorophylla* And.

As already mentioned, ANDERSSON regarded HOOKER's *S. villosa* in 1858 as only a variety of *S. glauca* L. He said: "Haec forma speciei maxime vegeta videtur," and in his short description (in Öfv. K. Vet.-Akad. Förh. **15**:109) we read: "foliis tenuioribus, supra (sic!) glaucis, sparse pilosis, elevato-venosis, stipulis subpersistentibus lanceolato-linearibus; amentis sat longis erectis laxiusculis, subrarifloris . . . ." The same diagnosis is repeated in Sal. Bor.-Am. 22, and in Walp., Ann. Bot. **5**:753. 1858. The statement "foliis supra glaucis" is certainly a misprint for "subtus glaucis," or it may be that a whole sentence has been omitted. Unfortunately, ANDERSSON did not cite a specimen, but his description scarcely fits the Rocky Mountain material collected by DRUMMOND. Ten years later ANDERSSON (in DC. Prodr. **16**^{2}:281) proposed a new hybrid *S. glaucops*,[3] which he placed without a number between 107. *S. glauca* and 108. *S. desertorum*, and of which he describes 2 "modifications," namely, var. *villosa*, being identical with his former *S. glauca* var. *villosa*, and var. *glabrescens*, which he based on specimens collected by BOURGEAU in the Rocky Mountains, and with which I shall deal later.

ANDERSSON referred to his *S. glaucops villosa* not only HOOKER's *villosa* and his own *S. glauca villosa*, but also *S. villosa* Seemann ("Voy. of Herald. p. 39. 54") and "*S. cordifolia* Hook. Fl. Boreal.

[3] It ought to be mentioned that this species has been entirely misunderstood by M. J. JONES, Willow Fam. Great Plat. 16. 1908. The author says of his study: "This work, on western willows, is put forth tentatively in order to clear up doubts. . . . ." But he certainly succeeded in greatly augmenting the existing confusion in regard to many species. There are scarcely 2 willows better distinguished than *S. glaucops* And. and *S. subcoerulea* Pip., which JONES makes synonyms.

amer. p. 152. p.p. (non Pursh)." SEEMANN's plants came from western Eskimaux-Land (Northwestern Alaska from Norton Sound to Point Barrow), while HOOKER's specimens to which ANDERSSON alludes were collected in Labrador. The Rocky Mountain specimens mentioned by HOOKER are not included, as they had already been described by ANDERSSON as *S. subcordata* (*S. arctica* var. *subcordata* Schn., see my first paper). ANDERSSON's main description of *S. glaucops* fits best Seemann's specimens, and such forms as *S. villosa acutifolia* Hook., of which ANDERSSON made no mention at all either in 1858 or in 1868. According to the rules of nomenclature the name *S. glaucops* has to be applied to the *S. glauca* of Alaska, the Yukon, and the Mackenzie district if further investigations should prove that these forms can be regarded as a distinct species. Unfortunately, this name has been used by RYDBERG (1899) and BALL (1909) to designate a more southern form of the Rockies, for which I use the name *S. pseudolapponum* v. Seem. (see later). When BALL first treated this form in 1899 (Trans. Acad. Sci. St. Louis **9**:88) he expressly said: "Our Rocky Mt. form was included under *S. glauca villosa* by Mr. BEBB, but it is certainly not the *S. villosa* Don described by HOOKER (Fl. Bor.-Am. **2**:144) and later published by ANDERSSON as *S. glauca villosa* (Sal. Bor.-Am. 22). That had long leaves and thick aments 2–3 inches long, being thus more closely related to the European *S. glauca*," and (*l.c.* 89) BALL designates *S. glauca* var. *villosa* And. (*S. villosa* Barr., *S. glaucops* And.) as a form of which "full discussion must be deferred until more abundant material is accessible." He adds that "HANSEN's no. 800, Fl. Sequoia Reg., 1892, is a plant which nearly answers the original description," but in my opinion HANSEN's specimen differs widely from it, and belongs to *S. californica* Bebb, a fact suggested by BALL himself.

According to RYDBERG (1899), *S. glauca* is "apparently rare in America, and probably confined to the extreme northeast portion." Nevertheless, he cites, besides specimens from western Greenland and Labrador, "Alaska: Nurkagak, 1881. McKay," meaning Nushagak in the Bristol Bay. This specimen is referred by COVILLE to *S. glauca*. Furthermore, in 1901, RYDBERG described a *S. Seemannii*, the type of which had been "collected at Dawson

by R. S. WILLIAMS, June 11, 1899, a more mature specimen June 12. Also collected by SEEMANN on Chamisso Island, 1851, no. 1873, and Kotzebue Sound and Norton Sound, 1849, no. 1423." He accompanied his description with the following remarks: "SEEMANN's specimens, cited below, were named by HOOKER *S. glauca* var. *macrocarpa*, but the plant is neither *S. macrocarpa* of TRAUTVETTER nor that of NUTTALL; it is related to the former, but not to the latter. *S. macrocarpa* Trautv. (*S. glauca macrocarpa* Ledeb.) is described as having sessile stigmas and fuscous bracts; it probably does not occur in America." In the original description of *S. macrocarpa* Ledeb. apud TRAUTVETTER (in Nouv. Mém. Soc. Nat. Mosc. **2**:292. 1832) I fail to find the statement that the stigmas are sessile; this part of the diagnosis runs: "stylo basin usque bipartito, stigmatibus bifidis." TRAUTVETTER compares in detail *S. glauca* and *S. macrocarpa*, and attributes to the latter the following characters: "frutex pedalis prostratus," "folia majora, acuminata, juniora jam fere prorsus glabra," and "pedicellus interdum fere longitudine ovarii." The same statement is given for *S. glauca* β *macrocarpa* Trautvetter in LEDEBOUR, Fl. Alt. **4**:281. 1833. Judging by those characters the American form in question cannot be identified with this var. *macrocarpa*, but better agrees with what TRAUTVETTER (1832) regarded as typical *S. glauca*, and named *S. glauca* var. *microcarpa* Ledeb. in 1833. Here TRAUTVETTER says, after having given an ample description of the specimens from the Altai, "exemplaria altaicis simillima Cl. Eschscholtz legit ad Cap. Espenberg."

As already stated, it is difficult to decide at the present status of our knowledge of the Old World forms of *S. glauca* whether some of them are identical with the American forms. So far as I can judge by TRAUTVETTER's descriptions and the material I have seen from Asia, I am not convinced that the forms of Northwestern America can be regarded as representing the typical *S. glauca* or one of TRAUTVETTER's varieties. A keen and careful observer like COVILLE, in 1901, said: "There is a tendency among American willow students to exclude *Salix glauca* from the North American flora, but our Alaskan specimens show so close an agreement with some European material of this species that I am unwilling to

separate them." He adds that he is not "able to find in the description [of *Seemannii*] a record of any characters that serve to distinguish the specimens assigned to the latter species from forms of *glauca* found in America and Europe." I agree with COVILLE that the North American forms are very similar to those of *S. glauca*, but they are in my opinion not fully identical with the typical *S. glauca* L. s. str., the characters of which I have already indicated. In looking over the copious and well collected American specimens before me, I hesitate to designate them as typical *S. glauca*, nor am I willing to regard them as a separate species until a closer study of this circumpolar willow has convinced me of one fact or the other. Those specimens exhibit a great degree of variability in the shape and size of the leaves, in the amount of pubescence, in the length of the aments, and in the characters of the flowers. As a whole they seem to differ from the typical *S. glauca* by the usually well developed stipules, by the longer pedicels of the fruits which normally are from one-half to twice longer than the gland, and by the tendency of the filaments to become almost glabrous. Judging by COVILLE's statement with regard to *S. reticulata*, that "in all the other Alaskan willows the filaments are glabrous throughout," I supposed that this fact might furnish a good character to separate specifically the American *S. glauca* from the European-Asiatic species, but a close investigation of all the male specimens at my disposal convinced me that the filaments are always more or less hairy at their base. Specimens like nos. 3369 or 3373 of TRELEASE and SAUNDERS, which apparently have entirely glabrous filaments, do not seem to be pure *S. glauca*, and the American form probably hybridizes with other willows as freely as does the European one.

If we regard the American *S. glauca* as a distinct variety, we have unfortunately to use the varietal name *acutifolia* given by HOOKER to his variety of *S. villosa*, because it antedates ANDERSSON's *S. glauca villosa* by almost 30 years, and apparently represents a rather extreme form with narrowly lanceolate leaves. I regard my determinations as rather provisional, and I am not convinced that my present limitation of the Northeastern American forms of *S. glauca* can be taken as a definite solution of this difficult question.

As previously stated, ANDERSSON also described a *S. glaucops* var. *glabrescens* from specimens collected by BOURGEAU in 1858, probably in Alberta, Rocky Mountains district, near the Bow River Pass. The description runs thus: "*β*, *glabrescens*, amentis crassis vulgo multifloris, foliis rigidioribus supra sparse pilosis demum glabris subtus sat intense glaucis." Furthermore he said: "quam autem *glabrescentem* appelavi longius distat et *S. chlorophyllam* (e typo *S. phylicifoliae*) non parum revocat, foliis glabris supra lucidis et nervosis subtus glaucis reticulatis, amentis multo brevius pedunculatis et capsulis distinctius pedicellatis. Ad *S. desertorum* manifestissimum praebet transitum." There is a specimen of BOURGEAU's in Herb. G. which, in my opinion, represents a co-type of ANDERSSON's variety. It bears the label of PALLISER's Expedition and is named "*S. glauca* L.×*pallida glabrata* And." ANDERSSON not infrequently changed a name in his publication after having marked the herbarium sheets in a different way. The specimen consists of 2 pieces of well fruiting branchlets. The aments measure up to 5:1.5 cm. and do not differ from typical var. *acutifolia* (syn. var. *villosa*) as collected by BOURGEAU and DRUMMOND in the Rockies. The co-type before me apparently represents a less glabrescent form, and it approaches much the other variety, with which it seems connected by a whole series of intermediate forms. The most glabrous ones I have seen were collected in the vicinity of Dawson, Yukon Territory. I deem it best to give the following characteristics and synonomy of the two varieties:

1. S. GLAUCA var. **acutifolia,** comb. nov.—*S. villosa* Barratt apud HOOKER, Fl. Bor.-Am. **2**:144. 1839, p.p.; SEEMANN, Bot. Voy. Herald 39 (Fl. W. Eskimaux Land). 1852.—*S. villosa* var. *acutifolia* Hook., Fl. *l.c.*—*S. glauca* var. *villosa* And. in Öfv. K. Vet.-Akad. Förh. **15**:127. 1858, p.p.—*S. glaucops α villosa* And. in DC. Prodr. **16**^{2}:281. 1868, p.p.—*S. glauca* Richardson in FRANKLIN, Narr. Jour. Polar Sea, Bot. App. 753. 1833, non L.; COVILLE in Proc. Wash. Acad. **3**:321. pl. 39. 1901.—?*S. glauca subarctica* Kjellman, Fanerog. Vest-Eskim. Land 51. 1883, in Nordenskiöld, Vega Exp. Vet. Takttag. **2**:51. 1883, non Ldstr.—*S. Seemannii* Rydbg. in Bull. N.Y. Bot. Gard. **2**:164. 1901.—*S. glauca*, var. *Seemanii* Ostenfeld in Vid.-Selsk. Skrift. I. Math.-Nat. Kl. 1909.

no. 8:34 (Vasc. Pl. Arc. N. Am. Gjöa Exp. 1904–6). 1910.— Frutex erectus, 0.5–1.5 m. altus; ramuli novelli dense alboserico-villosi vel villoso-tomentosi, hornotini vix vel paullo glabrescentes, annotini biennesque pl. m. purpureo-brunnei vel epidermide secedente flavo-cinereo-brunnei, sparse vel partim villosulo-tomentosi vel glabrati, interdum pl. m. nitiduli, circ. 2–3 mm. crassi, vetustiores similes, glabri, saepe castanei; gemmae ut videtur ovatae, ventre pl. m. applanatae, apice saepe rostratae, obtusae, initio dense pilosae, demum fere glabrae, purpureo-brunneae, 4–5 mm. longae. Folia adulta pl. m. chartacea vel papyracea, inferiora minora (vel pedunculorum) elliptica, obovato-oblonga, oblanceolata, vel obovalia, basi obtusa vel vulgo cuneata, apice obtusa ad subacuta vel subrotunda et apiculata, integerrima, minimis margine saepe tenuiter glanduloso-denticulatis exceptis circ. 2:0.8 ad 3.5–4:1.5 cm. magna, superiora majora late lanceolata vel oblanceolata, elliptico- vel obovato-oblonga, ovato- vel obovato-elliptica, apice obtusa vel acuta vel fere breviter subacuminata, basi obtusa vel vulgo subito vel sensim cuneata, 5:1.5 vel 4.5:2 ad 7:2.3 cm. magna, surculorum saepe late ovato- vel obovato-oblonga vel late elliptica, 7:3 ad 12:6.5 cm. magna, maxima interdum margine distincte breviter denticulata, superne novella adpresse sericeo-villosa, etiam adulta pl. m. villosula vel vulgo glabrescentia, ad costam marginemque tantum distinctius villosula, estomatifera, costa nervisque lateralibus planis vel subimpressis, nervillis satis indistinctis, subtus novella densius quam superne sericeo-villosa, etiam adulta pl. m. adpresse sericea vel villosula, valde discoloria, albescentia vel glaucescentia, costa flavescente nervisque lateralibus utrinque circ. 6–10 pl. m. elevatis, nervillis saltem in foliis adultis tenuiter prominulis. Petioli 3–12 mm., in surculis ad 2 cm., longi, superne sulcati, ut ramuli pilosi, vel dein glabrati, flavescentes. Stipulae ut videtur semper evolutae, in ramulis vegetis maximae, pl. m. lineari- ad semi-cordato-lanceolatae, rarius semiovato-rotundae, satis distincte glanduloso-denticulatae, ut folia pilosa, petiolo duplo breviores ad $\frac{1}{3}$ vel fere duplo longiores, maximae surculorum ad 3:1 cm. magnae. Amenta coetanea vel subserotina, pedunculos ut rami pilosos foliatos terminatia, satis longe cylindrica, sub anthesi vulgo densiflora, rhachide villosa;

mascula pedunculis 0.5 ad 1.5 cm. longis exceptis (2–)2.5–4 cm. longa et 0.8–1 cm. crassa; bracteae oblongae vel obovato-oblongae, apice obtusae vel rotundae, rarius acutiusculae, concolores et stramineae vel ut videtur saepius pl. m. bicolores, apice purpurascentes vel fuscescentes, utrinque villosae et apice pl. m. sericeo-villosae; stamina 2, filamenta libera (rariter ad basim paullo connata), basi vel fere ad medium pl. m. pilosa (an interdum glabra?), adulta bracteis duplo ad 2.5plo longiora; antherae ut videtur ellipsoideae, flavae vel initio roseae; glandulae vulgo 2, interdum dorsalis non visa; ventralis late ovato-rectangularis vel oblongo-conica, apice truncata vel apice incisa vel bi(–3)fida, quam bractea 2–2.5plo brevior; dorsalis vulgo distincte minor et angustior, integra; feminea sub anthesi vulgo 2–4:0.8–1 cm. magna, fructifera laxiora satis elongata 3.5 ad 7 cm. longa et circ. 1.5 cm. crassa, pedunculis 1–3 cm. longis exclusis; bracteae oblongae, obtusae, iis florum mascul. similes; ovaria sub anthesi ovoideo-oblonga, subsessilia vel pedicello glandula breviore suffulta, dense albo- vel griseo-villoso-tomentosa; styli distincti, subcrassi, integri vel apice bifidi vel fere bipartiti brachiis saepe divaricatis quam stigmata bifida oblonga vix vel circ. ½plo longiores; glandula 1, ventralis, pl. m. late ovato-rectangularis et integra vel bifida ad bipartita, bractea circ. duplo brevior; fructus maturi ellipsoideo-conici, ut ovaria vel laxius villosi, pedicello vulgo distincto glandulam interdum ½ (rarius 2plo) superante excluso (6–)7–8(–9) mm. longi, valvis apertis paullo recurvatis.

This variety seems closely connected with the following one by intermediate forms, although the extremes look rather different.

S. GLAUCA var. **glabrescens,** nov. comb.—*S. glaucops*, var. *glabrescens* And. in DC. Prodr. **16**²:281. 1868.—*S. Austinae* Rydbg., Fl. Rocky Mts. 198. 1917, non Bebb, pro parte.—Frutex ut in var. *acutifolia* descriptus, ab ea signis sequentibus praecipue differt: ramuli novelli vulgo minus dense villosi, hornotini pl. m. glabrescentes, rarius ab initio fere glabri vel citissime glabri, annotini biennesque glabri vel sparse (saltem partim) pilosi, olivaceo-purpurascentes, pl. m. nitiduli; folia apice saepe magis acuta, margine (saltem inferiora) saepius sed satis obsolete denticulata, majora

obovato-elliptico-oblonga vel late elliptico-lanceolata ad 6–7:2–2.5 cm. magna, superne saepe ab initio glabra, vividius colorata, subtus novella tantum pl. m. dense villosa, citius quam in *acutifolia* glabrescentia, adulta fere glabra vel parce pilosa, albescentia; filamenta basi sparsius pilosa, bracteae florum satis glabrescentes; amenta fructifera in co-typo ad 5 cm. longa et 1.5 cm. crassa, basi vix laxiflora, sed vulgo satis variabilia et basi pl. m. laxiflora; fructus pl. m. glabriores vel basi glabri.

So far as I can see, the range of var. *glabrescens* extends through the Rockies of Alberta and British Columbia to the northwest corner of this state and adjacent Alaska northward into the Yukon Territory, in the vicinity of Dawson. It probably occurs also in Alaska and the eastern Northwest Territories together with var. *acutifolia*.

As mentioned in the synonymy, RYDBERG has used the name *S. Austinae* Bebb as the specific designation for *S. glaucops glabrescens* And., but he also determined forms of a different origin as *S. Austinae*. This species had been proposed by BEBB in Watson, Bot. Calif. 2:88. 1879, but BEBB himself stated (in BOT. GAZ. 16:106. 1891) that it forms a mixture of 3 species, including *S. Lemmonii* Bebb and *S. lasiolepis* Bth. The female piece only represented an apparently new willow, and it is described as having "sessile aments appearing before the leaves, with small early deciduous bracts, dark scales, clothed with silky hairs." I fail to see how the name given to such a different form can be applied to *S. glauca glabrescens* even if we raise this variety to a specific rank.

Before it is possible to define correctly a variety like *glabrescens* we have to become much better acquainted with *S. pseudolapponum*, the so-called *S. glaucops* of the Rocky Mountain floras.

A few words must be said about the "*glauca*" of northeastern arctic America and of Greenland. I have to take into consideration the willows of Greenland because the flora of (at least western) Greenland is essentially American, and the forms of Labrador and northeastern arctic Canada cannot be properly understood without elucidating those of Greenland. The best enumeration of Greenland's *Salix* has hitherto been given by LANGE in his Conspectus Fl. Green. pt. 1. 1880 and pt. 2. 1887. In 1880 he cites not less than 5 varieties under *S. glauca*, which I cannot interpret correctly without comparing the specimens LANGE had before him, which are preserved in the herbarium at Copenhagen. So far as I can judge by the figures and quotations cited by LANGE, none of those varieties

seems to be identical with the typical *S. glauca* or any of the forms of Northeastern Canada. The specimens from Labrador and Greenland referred to *S. glauca* by RYDBERG do not belong to it or are at least very uncertain in their relationship. There is only one form before me which seems to be closely connected with the true *S. glauca*, and of this I shall say something under *S. anamesa*, after having discussed the types and relatives of *S. desertorum*, *S. pseudolapponum*, and *S. cordifolia*.

2. S. DESERTORUM Richardson, Bot. App. in Franklin, Narr. Jour. Polar Sea 753 (reprint p. 25). 1833; ed. 2.765 (reprint p. 37). 1833; HOOKER, Fl. Bor.-Am. **2**:151. 1839, pro parte; ANDERSSON in DC. Prodr. **16**²:281. 1868, excl. var.; RYDBERG in Bull. N.Y. Bot. Gard. **1**:272. 1899; excl. specim. Drummond.; BALL in Trans. St. Louis Acad. Sci. **9**:85. 1899, pro parte.—*S. glauca* **S. desertorum* And. in Öfv. K. Vet.-Akad. Förh. 127. 1858.—This is one of the most misunderstood willows, and I am sorry to say that I have not yet been able to explain it sufficiently. The type was collected by RICHARDSON at old Fort Franklin on the Mackenzie River. I have before me a photograph and fragments of the type material preserved in the Hookerian Herbarium at Kew, which show that the specimens distributed by BARRATT under no. 70 are identical with it. Unfortunately all the specimens have only young flowers and leaves except a few fragments of a fruiting catkin of the previous year in the Kew specimen. HOOKER (1839) referred to *S. desertorum* also specimens collected by DRUMMOND, and BEBB (apud ROTHROCK in Wheeler, Rep. U.S. Geol. Surv. West of 100th merid. **6**:Bot. 241. 1878) apparently took DRUMMOND'S no. 657 for the typical *S. desertorum*, as did BALL (1899) on BEBB'S authority. RYDBERG (1899) said: "It is evident that Mr. BEBB did not exactly know the true *S. desertorum*," and he stated that it is DRUMMOND'S no. 658 that "matches RICHARDSON'S specimens exactly." Both of DRUMMOND'S specimens are before me. There is no doubt that no. 657 belongs to *S. brachycarpa* Nutt. (*S. stricta* Rydbg.), but I am likewise convinced that no. 658 is not identical with RICHARDSON'S type. This number consists of two young male and female branchlets, and it differs chiefly by the pubescence of the young parts (the lower surface of the leaves, etc.) which is

mixed with minute fulvous hairs, by the rather long pedicel of the young ovaries which is about twice as long as the gland, and by the absence of a dorsal gland in the male flowers. At present I am unable to determine this plant correctly, as we do not know much of the *Salix* of the regions where DRUMMOND[4] collected.

ANDERSSON first mentioned *S. desertorum* quasi as a subspecies of *S. glauca*, and he said: "Insignis sane est forma, in orbe vetere quantum scio, non crescens. . . . Transitus vero ad normalem *S. glaucam* non nunquam reperti; videtur itaque hujus modificatio frigida." In 1868 he kept *S. desertorum* as a species, and added the following varieties: α, *elata*, β, *stricta*, and γ, *fruticulosa*. The last two are, in my opinion, nothing but *S. brachycarpa* Nutt. The first is based on specimens collected by DRUMMOND in the Rockies, but no number is given. It is described as "frutex 4–5-pedalis, ramis subsimplicibus crassis rufescentibus, foliis basi subangustatis supra glabris venis modice impressis subtus demum glabrescentibus amentis semipollicem longis." This description rather fits the male pieces of DRUMMOND'S no. 660 in herb. G., while the female piece of this number can hardly be distinguished from *S. brachycarpa*. This male no. 660 is the only one of DRUMMOND'S specimens I have seen that may belong to the true *desertorum*. This seems to be a species confined to the northern parts of Alberta and the Northwest Territories, but the young types are not sufficient to give a correct idea of the species. There is another specimen, however, preserved in the Torrey herbarium at New York and labeled "*Salix desertorum* Fl. Bor. Am." It consists of 4 pieces; a fruiting branchlet in the upper left corner of the sheet, a female one underneath it, and 2 male pieces at the right hand. The fruiting branchlet is undoubtedly *S. brachycarpa*, while the male and female material may be identical with the true *S. desertorum*. The male branchlet seems to represent a late flowering stage, and it bears

[4] According to J. MACOUN (Cat. Can. Pl. I. preface p. viii. 1883), DRUMMOND "explored the whole country from the Red and Assiniboine Rivers by the North Saskatchewan and Athabasca to the Rocky Mountains." He also "collected in the main range of the Rocky Mountains, between lat. 52–56°, and particularly in the part about the head of the Smoky River, a tributary of the Peace." Dr. J. M. MACOUN is spending the summer of this year in these regions and will probably bring back many of the forms collected by DRUMMOND from their original localities.

rather far advanced leaves, the largest of which measure up to 4 cm. in length and 12 mm. in width. They are narrowly elliptical, acute at both ends, finely puberulous on the midrib and on some of the veins above, and glaucescent and almost wholly glabrous beneath, with an entire, ciliated margin. To the true *S. desertorum* may also belong (at least partly) the following 2 specimens collected by J. W. TYRULL: Hudson Bay, west of Chesterfield Inlet, September 2, 1893 (no. 1711 O., f., fr.), and between Lake Athabaska and Chesterfield Inlet, July-August 1893 (no. 1712 O., m., f.). Both numbers consist of several small pieces apparently taken from different plants, and it is impossible to judge them properly.

I think it best to give the following description of the type material, because I shall not be able to insert *S. desertorum* into the key. Frutex erectus sesquipedalis (fide RICHARDSON), habitu ut videtur *S. pseudolapponum* non absimilis; ramuli novelli satis dense, rarius laxius albo-sericeo-villosi, hornotini paullo glabrescentes, annotini subglabriores vel tantum partim pilosi, brunnescentes vel interdum ut vetustiores vulgo nondum perfecte glabri purpurascentes et nitiduli, adulti flavo-brunnei, epidermide griseo secedente obtecti; rami cinereo-badii vel nigrescentes; folia speciminum typicorum valde juvenilia vel vix semi-evoluta membranacea, elliptico-lanceolata vel obovato-lanceolata (ex auctore "exacte elliptica"), apice obtusa vel vulgo pl. m. acuta, basi subito vel sensim in petiolum angustata, superiora integerrima vel tantum versus basim parce et obsolete denticulata, infima fere circumcirca tenuiter glanduloso-subdenticulata, maxime evoluta ad 3:0.9 cm. magna; superne ab initio glabra vel sparse (ad costam densius) villosula, in sicco subnigrescentia, valde indistincte subinciso-nervata et reticulata, stomatibus (an semper?) instructa, subtus pl. m. discoloria, glaucescentia, pruinosa, magis (saltem inferiora) sericeo-villosa sed cito satis glabrescentia pilis adpressis difficile recognoscentibus (tardius evoluta ut videtur distinctius pilosa); petioli nondum satis evoluti, vix ad 5 mm. longi, laxe sericei; stipulae nullae vel vulgo pl.m. evolutae, minimae vel parvae, maximae lanceolatae, glanduloso-denticulatae, parce pilosae, petiolis circ. $\frac{1}{3}-\frac{1}{2}$ breviores; amenta coetanea vel subserotina, cylindrica, ramulos breves foliatos sub anthesi vix ad 1 cm. longos terminantia, rhachide villosa;

mascula 2–3.5 cm. longa et circ. 8 mm. crassa, densiflora; bracteae oblongae ad obovatae, apice obtusae rotundataeve, stramineae vel flavo-brunneae (vix fuscae), pl.m. laxe praesertim ad apicem sericeo-villosae vel distinctius sericeae, extus saepe glabrescentes; stamina 2 filamentis liberis basi pl.m. pilosis dein bracteis duplo superantibus; antherae flavae(?), ellipsoideae, satis parvae; glandulae 2, ventralis ovato-conica, apice truncata, interdum pl.m. bifida, bractea 2.5–3plo brevior, dorsalis minor, angustior, vulgo integra; feminea sub anthesi 1.5–3:0.7 cm. magna; bracteae ut in masculis, sed brevius villosae, vix sericeae; ovaria oblongo-ellipsoidea, albo-villoso-tomentosa, sessilia vel subsessilia, styli sub anthesi breves, stigmatibus brevibus oblongis bifidis vix longiores, integri vel apice breviter bifidi; glandula 1, elongato-conica, apice truncata vel subretusa, interdum leviter incrassata, bractea duplo brevior; fructus tantum pauci anni praeteriti ex herbario Kewensi visi ellipsoideo-conici, subrostrati, circ. 6.5 mm. longi, satis glabrescentes vel tantum basi pedicelloque quam glandula subduplo breviore pilosi.

3. S. PSEUDOLAPPONUM v. Seemen in Bot. Jahrb. 29. Beibl. **65**: 28. 1900; RYDBERG, Fl. Rocky Mts. 197. 1917.—*S. glauca villosa* Andersson in Öfv. K. Vet.-Akad. Förh. **15**:127. 1858, pro parte; BEBB in Coult., Man. Bot. Rocky Mts. 338. 1885, pro parte max.—*S. glaucops* Rydberg in Bull. N.Y. Bot. Gard. **1**:270. 1899, p.p.m.; BALL in Coult. and Nels., New Man. Rocky Mts. Bot. 135. 1909, p.p.m.—*S. desertorum* Ball in Trans. St. Louis Acad. Sci. **9**:85. 1899, pro parte.—*S. glauca* var.? Ball, *l.c.* 88, p.p.—*S. Wolfii* var. *pseudolapponum* Jones, Willow Fam. 17. 1908, prob. tantum ex parte.—To understand this species it is necessary to compare the explanations given under *S. brachycarpa* and *S. desertorum*. As I have already explained under *S. glauca*, the names *S. glaucops* and *S. glauca villosa* And. cannot be used for those forms which are named *S. glaucops* by BALL and also by RYDBERG, who keeps *S. pseudolapponum* as a different species. In his *Flora Colorado* 93. 1906, he distinguished them in the key by the following characters: "Leaf-blades oblong or linear-oblong; bracts obovate; shrub depressed," *S. pseudolapponum*, and "leaf-blades oblanceolate or obovate-lanceolate; bracts oblong; shrub not depressed,"

S. glaucops. In his *Fl. Rocky Mts.* 190. 1917, he says the same and adds that the leaves are 2–3 cm. long in the first, while they measure 3–6 cm. in length in the second species. The largest leaves of *S. pseudolapponum* I have seen measured up to 5.5:1.8 cm., but usually they are not longer than 4–4.5 cm., and from about 1.5 to 2.2 cm. wide. RYDBERG apparently refers to his *glaucops* some forms which I do not regard as belonging to it, giving as the range "Alta.—N.M.—Utah—Calif.—Yukon," while he restricts *S. pseudolapponum* to Colorado. The type of this species (*Baker, Earle*, and *Tracy*, no. 300½, male) came from Mount Hesperus in the La Plata Mountains in southwestern Colorado, and represents a young flowering stage which naturally looks rather different from a fully developed specimen with old fruits. After having compared an extensive series of well collected specimens, I fail to see how it is possible to separate specifically this southern Colorado plant from the other forms in Colorado, where the species seems to have its headquarters, but the typical *S. pseudolapponum* may represent a dwarfed more alpine form of the so-called *S. glaucops*, which, therefore, should be distinguished as a new variety of *S. pseudolapponum*. There are several forms which otherwise seem to be identical but do not have stomata in the upper leaf epidermis, with which the typical *S. pseudolapponum* is always provided, differing in this respect from *S. brachycarpa* (see later). So far as I can judge by the copious material before me, these two species seem to hybridize rather freely, and I cannot explain certain forms in any other way. We need, however, a much more careful study of these forms in the field to decide the question whether these hybrids are common. From New Mexico I know *S. pseudolapponum* only in a somewhat uncertain sterile form from Taos County, Costilla Valley (leg. *E. O. Wooton*, September 4, 1914), and from Wyoming I saw no specimen but *Nelson's* no. 7831 from the Medicine Bow Mountains in Albany County. From farther northward I saw specimens from Teton County, Montana (leg. *C. S. Sargent* in 1883), and from Alberta, Sulphur Mountain, near Banff (leg. *A. Rehder*, August 8, 1904). Specimens from Lake County, Utah, need further observation, and I have seen nothing from Nevada, California, Oregon, or Washington which I can refer

to this species. A more intimate acquaintance with the *Salix* flora of these regions may lead me to a different opinion, but I hesitate to refer any doubtful forms to a certain species as long as I do not yet know all the other willows that may occur in the locality. Different species may sometimes look very similar at a certain stage of their development, and it needs a long time and the most scrupulous observation to become familiar with the variation of such polymorphic plants as the willows usually are.

4. S. BRACHYCARPA Nutt., North Am. Sylva **1**:69. 1843; RYDBERG, Fl. Colorado, 95. 1906; Fl. Rocky Mts. 197. 1917; BALL in Coult. and Nelson, New Man. R. Mt. Bot. 135. 1909.—*S. desertorum* Andersson in DC. Prodr. **16**²:281. 1868, saltem var. β et γ, non Richardson; BEBB apud ROTHROCK in Wheeler, Rep. U.S. Geog. Surv. west 100th Merid. **6**: Bot. 241. 1878; in Coulter, Man. Bot. R. Mts. 338. 1885, excl. var.; BALL in Trans. Acad. Sci. St. Louis **9**:85. 1899, pro parte.—*S. stricta* Rydbg. in Bull. N.Y. Bot. Gard. **1**:273. 1899; in Mem. N.Y. Bot. Gard. **1**:114 (Cat. Fl. Mont.). 1900.—The type of this graceful and well marked species was collected by NUTTALL in August 1818 "in the Rocky Mountain range, on the borders of the Bear River, a clear rapid brook cutting its way through basaltic dykes to the curious lake of Timpanagos, in New Mexico" (now the Great Salt Lake of Utah). No type specimen seems to be in existence, neither have I seen a plant from the type locality, but NUTTALL's ample and vivid description leaves no doubt as to the form of which he is speaking. ANDERSSON entirely misunderstood this species when (in 1867 and 1868) he added NUTTALL's name with ? as a synonym to his *S. longifolia argyrophylla angustissima*. ROWLEE (in Bull. Torr. Bot. Club **27**:248. 1900) seems to have been the first who reinstated NUTTALL's name for *S. stricta* (And.) Rydbg. As already stated, *S. brachycarpa* is apparently connected with *S. pseudolapponum* by intermediate forms, and in 1899, through his investigation of the Rocky Mountain material, BALL was led "to the conclusion that no rigid line can be drawn between the species as they are represented in that region." The extreme forms, he said, are widely divergent, but the numerous intermediates present an almost perfect gradation between these extremes. After all, this

is true only to a certain degree, and in my opinion the difficulty might be settled by regarding the intermediate forms as hybrids. Compared with each other, *S. brachycarpa* is distinguished by the denser and shorter, almost tomentose pubescence, the absence of stomata in the upper leaf epidermis, the shorter petioles, and the denser and shorter aments, especially the staminate with their minute globose anthers; while *S. pseudolapponum* seems to be well marked by the looser, almost a little silky-villose pubescence, the relatively longer petioles, the presence of more or less numerous stomata in the upper leaf surface, and by the somewhat looser male aments with rather stiff filaments and larger, more ellipsoid anthers. In the female aments the differences are often less obvious, and the differences given by BALL (1909) and by RYDBERG (1917) seem to me not borne out in fact.

I have seen no material of *S. brachycarpa* from Utah where the type had been collected. The species seems to be abundant in central Colorado from the Culebra Range in the south to the Medicine Bow Mountains in the north, and southern Wyoming, where it is frequently met with in the western part of the state and in or near the region of the Yellowstone Park, including northeastern Idaho and southern Montana. There is also a specimen before me from the Wallowa Mountains in southeastern Oregon (*Cusick*, no. 2298). From northern Montana its range extends in the Rockies to about 59° N. lat. and about 122° W. long., while in Alberta it occurs east of the Athabasca River through Saskatchewan to about 59° N. lat. I also have before me specimens from Churchill on the western shore of the Hudson Bay in Manitoba, and from the Gaspé Peninsula, which I am unable to separate even as a variety. At first sight the eastern forms seem to differ by the relatively shorter and broader leaves, the somewhat longer styles, and the longer ventral glands, but the same variations can be observed in western specimens. The form from Churchill (*J. M. Macoun*, no. 79156 O.), however, needs further observation. An uncertain form is represented by no. 74. Hb. H.B. and T. (fr.; N.), named *S. desertorum* var. *acutifolia*. It differs from the type by foliis subacutis ad 32:9 mm. magnis et praecipue amentis fructiferis satis laxifloris ad 3.5:1 cm. magnis.

Professor J. M. MACOUN, to whom I am indebted for much help, has collected in company with M. O. MOLTE a very interesting variety at Jasper Park, Alberta, on the low point running into the Athabasca River on the west side of the discharge of Beauvert Lake, July 30, 1917 (no. 95374, fr.; O.), which has glabrous or almost glabrous ovaries and fruits. It resembles *S. chlorolepis*, but the leaves of this species possess stomata in the upper surface which soon becomes glabrous, while in the western form the leaves are without stomata as in typical *S. brachycarpa* and have the same kind of pubescence. I also received a male specimen collected by J. M. MACOUN at the same place as the female type on July 23, 1918, and I am giving the following description of this variety for which I propose the name:

S. BRACHYCARPA var. **glabellicarpa,** nov. var.—Frutex ut videtur parvus, dense et breviter ut in var. *typica* ramosus; ramuli novelli vetustioresque ut in illa; folia conferta, anguste lanceolata, oblanceolata vel anguste elliptico-lanceolata, apice acuta vel subito apiculata, basi cuneata ad subrotunda, 7:2 ad 28:8 mm. magna, integerrima, sed infima pl.m. dense tenuiter glanduloso-denticulata, superne infimis exceptis pl.m. laxe villosula, vivide (?) viridia, estomatifera, costa rubescente vel flavescente subimpressa nervis vix visibilibus, subtus discoloria, glaucescentia, densius villosula vel inferiora initio magis sericea demum glabrescentia, costa prominente, nervis lateralibus utrinque ad 8 angulo acuto a costa abeuntibus vix vel paullo prominulis; petioli 1–3 mm. longi gemmis (an satis evolutis?) ad subduplo longiores; amenta pedunculo ad 5 mm. longo normaliter foliato suffulta; mascula circ. 8:5 mm. magna ceterum a typo non diversa; fructifera circ. 1:1 cm. magna, subglobosa; ovaria sessilia vel subsessilia, glabra vel ad apicem parce villosa, stylo integro, stigmatibus siccis parvis bifidis ad 2.5plo longiore coronata; glandula 1, ventralis, anguste ovato-conica, quam bractea obovata flavescens vel apice straminea utrinque laxe villosa subduplo brevior; fructus ovoideo-conici, 4–5 mm. longi, ut ovaria glabra vel apice sparse pilosa.

5. S. CHLOROLEPIS Fernald in Rhodora **7**:186. 1905, is a species peculiar to the Gaspé Peninsula, where it was detected in 1905 at the headquarters of Ruisseau du Diable on the famous Mount

Albert by *Fernald* and *Collins* (no. 59, m., f.; G., type). As FERNALD has already pointed out, it closely simulates in habit, bark, and foliage *S. brachycarpa*, but differs from it by its glabrous capsules and glabrous green bracts. There are, however, pubescent forms which look rather intermediate between *S. brachycarpa* and *S. chlorolepis*, and which have been taken for hybrids by FERNALD. The main difference between the two species is, in my opinion, found in the glabrousness of the filaments in *chlorolepis*, which are more or less pilose in *brachycarpa*, and in the presence of numerous stomata in the upper leaf epidermis of *S. chlorolepis*, while *S. brachycarpa* is entirely destitute of them. The pubescent form agrees well with typical *S. chlorolepis* in this respect, and cannot therefore be regarded as of hybrid origin; consequently I propose the following variety:

S. CHLOROLEPIS var. **antimima**,[5] var. nov.—*S. desertorum* Fernald in schedis, non Richardson.—A var. typica nonnisi differt ramulis foliisque novellis bracteis vulgo extus et ovariis omnino vel parte superiore pl.m. breviter cinereo-villosulis, foliis vulgo oblongioribus ad 3:1 cm. magnis etiam adultioribus subtus saepe sparse pilosis.

The following specimens have been examined: Quebec: Gaspé Peninsula, Mt. Albert, on wet serpentine slopes, July 23, 1906, *Fernald* and *Collins* (nos. 512, 512[a], f., 512[c], f., type, 512[b], f., 512[e], fr., 512[f], m.; G.); July 21, 1906, *Fernald* and *Collins* (nos. 518, m. paratype, 519, f; G.; no. 519 forma intermedia inter var. *typicam* et var. *antimimam* videtur et ab cl. FERNALD sub nomine *chlorolepis*×*desertorum* distributa est); ravine of cold brook, local, alt. 900 m., August 12, 1905, *Collins* and *Fernald* (no. 64, m., f.; A., N.; "ascending shrubs 3–6 dm. high"). There are indeed also some forms which have to be regarded as true hybrids between *S. chlorolepis* and *S. brachycarpa*. I shall deal with them on a later occasion.

6. S. NIPHOCLADA Rydberg in Bull. N.Y. Bot. Gard. 1:272. 1899; COVILLE in Proc. Wash. Acad. Sc. 3:322. *fig. 20.* 1901.—This species is still very little known. Its type was collected in 1892 by Miss E. TAYLOR in the Northwest Territories on the "Mackenzie River, at a point 30 miles north of the Arctic Circle." I did not see the type specimen, but the specimens mentioned by COVILLE (*F. Funston*, no. 185 and *E. A.* and *A. E. Prebble* no. 26),

[5] Derived from ἀντίμιμος, closely resembling.

who identified them with the type. The first came from the mouth of the Porcupine River in eastern Alaska, while the second was found near the mouth of the Seal River, 40 miles northwest of Fort Churchill on the Hudson Bay. Through the kindness of Professor J. M. MACOUN I saw also a small specimen collected by *F. Johansen* at Icy Reef in northeastern Alaska in 1914 (no. 164 or 93794 O.), which agrees well with *Funston* no. 185. *S. niphoclada* is "apparently nearest related to *S. stricta*" (*S. brachycarpa*) as stated by RYDBERG, while COVILLE was of the opinion that "the nearest relative to the species among American willows is *S. glauca*." In some respects *S. niphoclada* seems to approach *S. desertorum*, which, however, is still too insufficiently known. The statement in RYDBERG's description, "style 5 mm. long," is clearly a misprint for 0.5 mm. Owing to the lack of more copious material I am unable to elucidate the genetic relations between *S. desertorum*, *S. niphoclada*, and *S. brachycarpa*, nor can I properly define the taxonomic characters of the first 2 species. The most significant character of *S. niphoclada* seems to me the dense white silky-villose pubescence of the first season's shoots combined with the very short and densely silky petioles, which apparently do not exceed 2 mm. in length, while they are about twice as long and more obvious in *S. desertorum*. I am not inclined, therefore, to refer *Seton* and *Prebble's* no. 79 (no. 78300 O.) from the Mackenzie district, Artillery Lake, Last woods, to *S. niphoclada*, as it has been determined by BALL, as it seems to me more closely related to *S. desertorum*. We know, however, almost nothing of the *Salix* flora of the woodland region of the Northwest Territories, which must be an Eldorado for willows.

The following species which I propose is likewise characterized by the very short petioles, but it has an entirely different prostrate habit.

7. **S. fullertonensis**, nov. spec.—Frutex humilis depressus ramis ramulisque vulgo satis elongatis repentibus, floriferis ut videtur tantum adscendentibus. Ramuli novelli pl.m. villosuli vel breviter sericeo-villosuli, hornotini pl.m. glabrescentes, purpureo-brunnescentes, annotini fere glabri vel partim tomentelli, intense brunnescentes vel fere castanei, interdum subnitiduli, vix ultra 2 mm.

crassi, vetustiores epidermide secedente griseo obtecti; rami pl.m. cinereo-brunnei. Gemmae parvae, oblongae, obtusae, ellipsoideae vel fere ovato-globosae, flavescentes vel purpurascentes, initio pilosae, ut videtur vix ultra 2.5 mm. longae. Folia satis parva, adulta sub-chartacea, lanceolata, ovato- vel elliptico-oblonga, interdum anguste ovato-elliptica, elliptica, ovalia vel obovato-oblonga, apice vulgo acuta, rarius obtusa, basi pleraque rotundata, interdum late cuneata, margine integerrima vel rarius basim versus dentibus distantibus minimis glanduliferis paucis instructa, 1:0.4 ad 2.5:0.9 cm. magna vel (in no. 79161) ad 3 cm. longa et ad 1.1 cm. lata, superne novella pl.m. villosula vel etiam adulta nondum glabra, rarius fere ab initio glabra, ut videtur intense sed satis obscure viridia, costa paulo impressa nervis lateralibus subplanis, epidermide (an semper?) stomatifera, margine villosulo-ciliata, subtus discoloria, albescentia vel glaucescentia, pruinosa, novella et etiam adulta ut superne sericeo-villosula vel demum fere glabra, costa flavescente elevata nervisque lateralibus utrinque 5–8 prominulis ceterum satis indistincte tenuiter reticulata; petioli brevissimi, gemmis duplo breviores ad aequilongi, superne sulcati, pilosi, basi dilatati, vix ultra 2 mm. longi; stipulae vulgo evolutae, semicordatae vel semiovato-lanceolatae, acutae, pl.m. glanduloso-denticulatae, pilosae, 1–3 mm. longae. Amenta tantum feminea saepius fructifera visa, pedunculis (0.5–)1–2 cm. longis foliatis suffulta, cylindrica, sublaxiflora, sub anthesi circ. 1.2–1.5:0.5 cm., fructifera 2:1 ad 4:1.3 cm. magna; ovaria ovoideo-conica, dense griseo-villoso-tomentosa, sessilia, stylo brevi semipartito vel integro quam stigmata oblonga subbreviore ad sublongiore coronata; bracteae anguste oblongae, obtusae (in no. 79161 obovali-oblongae), brunnescentes, villosulae vel sericeo-villosulae, extus ad apicem interdum glabrescentes; glandula 1, ventralis, anguste ovato-conica, apice truncata, integra vel pl.m. bifida bipartitave, quam bractea circ. duplo brevior, in no. 79161 interdum glandula dorsalis parva visa; fructus anguste ovoideo-conici, ut ovaria vel minus dense tomentosi, sessiles vel subsessiles, 4–6 (vel ad 7) mm. longi.

TYPE LOCALITY: Eastern Canada, Hudson Bay, Fullerton, lat. 63°57′.

SPECIMENS EXAMINED: Canada: Hudson Bay, Fullerton, September 4, 1910, *J. M. Macoun* (79164, fr.; type; G., N., O.); July 10, 1904, *E. L. Borden*

(no. 63043, f.; N., O.; a young flowering stage); Ranken Inlet, lat. 62°45′, August 30, 1910, *J. M. Macoun* (nos. 79163, 79165, 79166, fr.; Cor., N., O.; identical with type); Bathurst Inlet, Arctic Sound, lat. 67° to 68° N., long. 109° to 111° W., August 25, 1915, *R. M. Anderson* (no. 467 or 93776 O., fr. im.; amentis satis laxifloris); Cape Eskimo, lat. 61° 05′, August 26, 1910, *J. M. Macoun* (no. 79161, fr.; Cor., N., O.; forma foliis fructibusque majoribus, saltem in specim. in O., stomata superne in foliis ut videtur deficientibus); Mansfield Island, September 1884, *R. Bell* (no. 24622, fr.; O.; specimen mancum incertum).

This is an interesting willow, and well marked in its typical form by the very short petioles of the small leaves, which are normally provided with stomata in the upper surface. It seems to be an entirely prostrate shrub with very slender creeping branches. Some of the forms I regard as *S. fullertonensis* or nearly related to it have been referred by RYDBERG to his *S. Macounii*, the type of which represents a very different plant, which I shall discuss under *S. cordifolia*.

The following specimens look to me more or less like forms that might be taken for *S. fullertonensis*×*S. groenlandica*. They seem to differ from *S. fullertonensis* in the following characters: gemmis majoribus ad 5:3 mm. magnis, foliis latioribus ovato- vel obovato-ellipticis ovalibus vel obovato-oblongis apice saepe plicato, acutis basi rotundis ad late cuneatis adultis margine sparse ciliato excepto glabris superne magis nitidulo-viridibus (stomatiferis) subtus paullo distinctius nervatis reticulatisque maximis ad 2.8:1.5 cm. magnis; petiolis ad 4 mm. longis sed gemmas bene evolutas non superantibus; amentis fructiferis fructibusque vix diversis, bracteis late obovatis pl.m. longius et magis sericeo-pilosis; fructibus sessilibus vel pedicello distincto glandulam interdum superante suffultis, circ. 7 mm. longis.

Hudson Bay: lat. 55–56°, barren shores, August 1886, *J. M. Macoun* (no. 18822, fr.; O.; ovariis sessilibus, bracteis sericeis, foliis distincte petiolatis, stomatiferis); Fullerton, September 4, 1910, *J. M. Macoun* (no. 79148 fr.; O.; 79167, fr.; Cor., G., N., O.; forma foliorum ut in *fullertonensi* sed petioli longiores, stomata desunt, ovaria subsessilia, glandulae saepe 2, bracteae sericeae); Ranken Inlet, lat. 62°45′, August 30, 1910; *J. M. Macoun* (no. 79162, fr.; Cor., G., N., O.; *S. groenlandicae* satis similis); Nottingham Island, 1884, *R. Bell* (no. 18820^{4} olim, = 54358 O., fr. juv.; satis ad *anglorum* spectans sed sine stomata); Digges Island, 1884, *R. Bell* (no. 18820^{3} olim, = 54359 O.; fragmentum, ut praecedens); Mansfield Island, 1884, *R. Bell* (no. 18820^{5} olim, = 54360 O.; fr.; probabiliter ut praecedens); James Bay mouth of Albany

River, July 25, 1904, *W. Spreadborough* (no. 62618, fr.; O.; magis ad *groenlandicam* spectat); Bathurst Inlet, Katur Point, lat. 67° to 68° N., long. 109° to 111° W., August 22, 1915, *R. M. Anderson* (no. 456 or 93775 O., f.; specimen mancum).

7. S. CORDIFOLIA Pursh, Fl. Am. Sept. **2**:611. 1814; TRAUTVETTER in Nouv. Mém. Soc. Imp. Nat. Mosc. **2**:298. *pl. 9* (De Salic. frig. Kochii). 1832; HOOKER, Fl. Bor.-Am. **2**:152. 1839, exclud. specim. Drummond.—*S. callicarpaea* Trautv., *l.c.* 295, *pl. 7*; RYDBERG in Bull. N.Y. Bot. Gard. **1**:270. 1899, quoad specim. labrad.—*S. planifolia* Hook., *l.c.* 150, quoad specim. labrad. saltem ex parte, probabiliter non Pursh.—*S. alpestris* c) *americana* Andersson in Öfv. K. Vet.-Akad. Förh. **15**:129. 1858.—*S. arctica* β *Brownei* 3° *fumosa* And. in DC. Prodr. **16**²:287. 1868, quoad pl. labr.—*S. glauca* Rydbg. in Bull. *l.c.* 271, quoad pl. labr.—*S. Waghornei* Rydbg., *l.c.*, pro parte; BRITTON and BROWN, Ill. Fl. ed. 2. **1**:604. *fig. 1486*. 1913.—*S. labradorica* Rydbg., *l.c.* 274, pro parte max.—PURSH's description of this species is very short and runs as follows: "*S.* depressa; foliis ovalibus subacutis basi cordatis integerrimis reticulato-venosis supra glabris, subtus pallidis nervo margineque pilosis, stipulis semicordatis." It was taken from a sterile plant cultivated "in Hort. Andersson." PURSH adds "in general habit it resembles *S. myrsinites*." Unfortunately there is no type left by PURSH, but a specimen from ANDERSSON's garden is preserved at Kew, of which I have not yet seen a photograph, but only a rough outline sketch in herb. G. The plant is next mentioned by FORBES (Salict. Wob. 277. *fig. 143*. 1829), who only translated PURSH's diagnosis. The leaf represented in *fig. 143* clearly shows a finely denticulate margin, and it looks much more like a leaf of *S. calcicola* Fern. I am unable to ascertain its identity. HOOKER said: "The plant named for me by Mr. BORRER, who is probably acquainted with the original plant cultivated by ANDERSSON, little deserves the appellation of *cordifolia*, its leaves being more frequently acute than retuse at the base. Many of the specimens approach very near the following" (*S. arctica* R. Br.). I have not yet seen the Labrador type of HOOKER's *cordifolia* collected by KOHLMEISTER. HOOKER also referred to this species specimens collected in the Rockies by DRUMMOND which represent *S. arctica*

subcordata (And.) Schn. (see my first paper). In the synonymy he mentioned *S. obovata* Pursh with a ?, but this species is described with "amentis subcoetaneis sessilibus" and does not apparently belong to our species. Furthermore, HOOKER'S *S. planifolia* is the same as *S. cordifolia* as to Miss BRENTON'S specimens from Labrador, of which I have a photograph and fragments before me. The sheet in herb. K. contains 6 specimens with fruits and adult female flowers of which only one (the middle piece at the left hand side) seems to belong to a different form on account of the presence of stomata in the upper leaf surface which are wanting in typical *S. cordifolia*.

Judging by the ample descriptions and the figures, TRAUTVETTER'S *S. cordifolia* and *S. callicarpaea* seem to represent nothing but two different stages of one species. His *S. cordifolia* is a poor specimen of a female plant with young flowers, while the figure of his *callicarpaea* shows a fruiting specimen collected by HERZBERG at Okak. Of RYDBERG'S *S. callicarpaea* I have only seen BELL'S Labrador specimen from "Nachhak" (Nachvak), a rather poor and sterile one (no. 18819, O.) which I cannot distinguish from typical *S. cordifolia*.

The other specimen cited by RYDBERG from Mt. Gaspé (probably meaning Mount Albert, Gaspé Peninsula), collected in 1882 by *Macoun* (no. 18826 O.), has not been available to me; it may belong to *S. anglorum* var. *kophophylla* Schn.

ANDERSSON (1858) divided *S. cordifolia* Hook. in his *S. subcordata* and *S. alpestris americana*, the latter representing the Labrador plant. In the *Prodromus* (1868) no mention is made of his *alpestris* and its 3 varieties of 1858, but only of the older *S. alpestris* Wulfen, which has nothing to do with it. *S. cordifolia* is cited under *S. arctica β Brownei* f. 1. *obovata* in the following sentence: "Huc *S. cordifolia* Pursh fl. 2. p. 611; Hook. fl. boreali-amer. 2. 152; Trautv. *l.c.* p. 298 t. 9 ex Labrador forsan etiam pertinet"; while on the following page under f. 3. *fumosa* of the same variety he says "Nonne haec potissimum: *S. cordifolia* Pursh fl. Amer. syt. 2.611. ?, Trautv. *l.c.* p. 298 (quae tamen stylo longissimo insignis videtur!)", and *S. callicarpaea* Trautv. is mentioned as a quasi-synonym under the last form. Besides this ANDERSSON says under *S. pyrenaica:*

"*S. cordifolia americana*, quam olim *S. Pyrenaicae* forma credidimus, vix a formis foliis tenuioribus nigricantibus *S. villosae* est distinguenda." This is a most curious statement, because he never referred *S. cordifolia* (or part of it) to *S. pyrenaica*, but he did propose (1858) a *S. alpestris* α *pyrenaica* besides his *alpestris americana*. Furthermore, under *S. glaucops* var. *villosa* ANDERSSON (1868) quotes "*S. cordifolia* Hook. Fl. Boreal.-amer. p. 152 p.p. (non Pursh)." These statements convey the impression that ANDERSSON was unable to interpret properly HOOKER'S species.

RYDBERG (1899) proposed the new name *S. Waghornei* for *S. cordifolia* Hook., not Pursh, without explaining why both are not identical, and without mentioning the fact that HOOKER in his *cordifolia* also included specimens of DRUMMOND from the "high parts of the Rocky Mountains." He says "Type in Herb. Torrey ('Fl. Am. Bor.')," which is a poor and almost valueless fragment consisting of one piece with a few remnants of fruits and another small one with undeveloped rather abnormal male catkins. The leaves of both have stomata in the upper epidermis, and the specimen looks more like a hybrid between *S. cordifolia* and *S. anglorum* than like *S. cordifolia*, which is certainly not identical with this "type." I am inclined therefore to use the name *S. Waghornei* for this supposed hybrid.

RYDBERG (1899) proposed 2 more species: *S. atra* and *S. labradorica*. Judging by the type before me, *S. atra* represents nothing but a form of *S. cordifolia*, of which I shall speak later, while *S. labradorica* is still a rather uncertain form because the female type (*Waghorn's* no. 36, 1892) as well as the male syntype (*Waghorn's* no. 31, 1892) differ from typical *S. cordifolia* by the presence of stomata in the upper leaf epidermis. The plants are too young to afford sufficient characters to recognize their real affinity. According to RYDBERG'S key, *S. labradorica* differs from the other species by its broadly ovate leaves "with white, villous almost permanent hairs, spreading in all directions," while in *S. Waghornei* and *S. atra* "the leaves are somewhat hairy when young, but the long white hairs are, as in *S. glauca*, appressed and parallel to the midrib." This kind of silky pubescence may be seen on the lower surface of the first (lowermost) leaves of almost all the forms in question,

while the later (superior) leaves bear more or less villous hairs "spreading in all directions," especially on the upper surface if the latter is not glabrous even when young, as is mostly the case with the young (first) leaves of the flowering branchlets. I have been unable to distinguish different forms by the amount or the character of the pubescence, and it is often difficult to determine properly young flowering specimens in the herbarium.

S. cordifolia is a widely distributed and variable species, its range extending from southern Greenland (about the 67th parallel) and Labrador (from the vicinity of Nachvak southward to the Strait of Belle Isle) westward to the western shores of the Hudson Bay (in var. *atra*) and southward to the Mingan Islands and the western Gaspé Peninsula,[6] northwestern Newfoundland, and in var. *Macounii* to the Bonne Bay region in western Newfoundland, but it is not yet reported from the Bay of Islands or the Blomidon range there. The forms of Greenland which I take for *S. cordifolia* are discussed under *S. anamesa*.

In Labrador it is often represented by the f. **atra** (Rydbg.), nov. forma, which seems to differ from the type only in its more oblong leaves which are acuter at both ends. The "turning black in drying" of the leaves mentioned by RYDBERG seems to me no character of taxonomic value because it is too often only a result of neglect in the press. I shall give an enumeration of the specimens referable to f. *atra* in my final book. At present I wish to draw the attention of collectors to another form for which I propose the name f. **hypoprionota**[7] nov. forma, because it chiefly differs from the type by its "foliis ex parte pl.m. serrato-denticulatis"; otherwise it seems to vary in the same manner as the type, being sometimes more or less prostrate, sometimes an erect shrub up to 1 m. in height. I refer to it the following specimens:

LABRADOR: Straits of Belle Isle: Blanc Sablon, limestone and calcareous sandstone terraces, by brook, August 1, 1910, *Fernald* and *Wiegand* (nos.

[6] There is a specimen from Mt. Albert collected August 27, 1882, by *Macoun* (no. 24509 O., with old male aments and mature leaves) which closely simulates the western *S. glauca* var. *acutifolia* from Alberta, and I cannot distinguish another of MACOUN'S specimens of August 2, 1882, said to be collected in "Gaspé, Que." with ripe fruits from the western *S. glauca*. But this has no number and I do not feel quite sure of the locality.

[7] Derived from ὑπό, somewhat, and πρίονωτός, serrated.

3224, f.; G.; foliis elliptico-oblongis paullo ad *f. atram* spectans; 3226 fr. type; G., "shrub 1 m. high"; foliis obovato-ellipticis ad 5.8:3 cm. magnis superne magis quam subtus laxe adpresse villosis vel inferioribus minoribus margine ciliato excepto glabris); Forteau, springy banks and damp hillsides, July 10, 1910, *Fernald* and *Wiegand* (nos. 3210, 3220, fr.; G.); Fox Harbor, near Battle Harbor, September 15, 1891, *Waghorne* (no. 11[a], fr.; Cor.); Ungava, along a river, July 1896, *Spreadborough* (no. 13687[a] O.; Cor.); Quebec: Mingan Islands, Ile St. Généviève, July 1, 1915, *H. St. John* (no. 90840 O., m., f.; G.); Island of Anticosti, Baie Sainte Claire, August 17–18, 1917, *M. Victorin* (nos. 4349, st., 4350, st., 4351, fr.; A.).

A distinct variety seems to be represented by the typical *S. Macounii* Rydbg., which came from Ellis Bay on Anticosti Island. RYDBERG referred to this species forms of different origin, but mostly those related to *S. fullertonensis* and *S. groenlandica*. It may be briefly characterized as follows:

7b. S. CORDIFOLIA var. **Macounii**, nov. var.—*S. Macounii* Rydbg. in Bull. N.Y. Bot. Gard. 1:269. 1899, quoad specim. typic. —*S. Rydbergi*[8] Heller, Cat. N. Am. Pl. ed. 2. 4. 1900.—*S. vaccinii-formis* Rydbg. in BRITTON, Man. Fl. N. St. Can. 319. 1901.—A typo praecipue differt foliis etiam adultis minoribus vix ultra 3:1.5 cm. magnis vulgo satis exacte ellipticis utrinque pl.m. acutis interdum margine pl.m. denticulatis adultis glaberrimis sed novellis pl.m. (saltem superne!) ut in typo villosis; amentis fructiferis vix ultra 3:1 cm. magnis.

TYPE LOCALITY: Island of Anticosti, Ellis Bay.

RANGE: Anticosti and northwestern Newfoundland, possibly also in Labrador and northern Ungava.

SPECIMENS EXAMINED: Quebec: Anticosti, Ellis Bay, September 7, 1883, *J. Macoun* (no. 18830 O., fr.; type).—Newfoundland: Ingornachoix Bay, damp rocky limestone barrens, near the sea level, August 4, 1910, *Fernald* and *Wiegand* (nos. 3203, f., fr., 3207, fr.; G.); dry rocky limestone barrens, near sea level, August 1, 1910, *Fernald* and *Wiegand* (no. 3218, fr.; G.; prostrate); August 2, 1910, *Fernald* and *Wiegand* (no. 3221, f., fr.; G.); Bonne Bay, barrens at the base of the serpentine table lands, August 27, 1910, *Fernald* and *Wiegand* (no. 3229, f.; G.); serpentine table land, alt. about 380 m., same date and collectors (no. 3230, fr.; G.).

[8] There is no reason according to the international rules or the Philadelphia code to change the name *Macounii* on account of the previous *S. Richardsonii* var. *Macouniana* Bebb, as HELLER in November 1900 and RYDBERG a few months later did, the latter not knowing of HELLER's name.

This variety needs further observation. It seems to be the prevailing one on Anticosti Island and in northwestern Newfoundland. Some more vigorous forms from Blanc Sablon and Forteau with more distinctly denticulate leaves might also be referable to it. RYDBERG'S type is a very glabrous specimen collected in September. Forms from Hopedale in Labrador (*Sornborger*, no. extra 1) and northern Ungava (*A. P. Low*, no. 24769 O.) are rather uncertain. Specimens like no. 3207 have the mature leaves entirely glabrous (except a few hairs on the margin), as in the type, while the young parts show a more copious pubescence similar to that of *S. cordifolia typica*.

There are other specimens which I cannot determine properly and which are worth further observation:

Newfoundland: Ingornachoix Bay, Pointe Riche, limestone barrens near sea level, August 4, 1910, *Fernald* and *Wiegand* (no. 3204, fr.; G.), forma foliis pl.m. orbicularibus vel ellipticorotundis satis ad var. *Macounii* spectans, fere ut in var. *typica* pilosa, sed floribus femineis glandula satis lata (fere ut in *groenlandica*) instructis et fructibus pedicello quam glandula sublongiore suffultis laxe puberulis, stylis brevibus stigmatibus brevibus bifidis vix longioribus, bracteis obovatis substramineis breviter pilosis.—*Quebec: Saguenay County, Archipel Ouapitagone, Ile Matchiatik*, sprawling on ledge, July 15, 1915, *H. St. John* (no. 90841 O., f.; G.), praecedente non absimilis.

A very uncertain form has been found by *St. John* on the Mingan Islands, Ile au Marteau (Eskimo Island), top of limestone shingle, July 28, 1915 (no. 90837 O., m., f.; G.): ramulis novellis perspicue dense albo-tomentosis, foliis semi-evolutis obovato-ellipticis ad 5:2.5 cm. magnis costa ex parte petioloque excepto glabris superne in epidermide stomatiferis inferioribus ut in f. *hypoprionota* denticulatis, stipulis semiovatis denticulatis glabris, floribus ut in *S. cordifolia* sed bracteis apice interdum leviter fuscis.

Lastly, there remains to be discussed a willow from western Greenland which seems most closely related to *S. cordifolia*, but which also considerably resembles *S. anglorum*, and has apparently been referred by most of the authors to *S. glauca*. I cannot include it among any of the species previously mentioned, but deem it best to propose a new species.

9. **S. anamesa**,[9] spec. nova.—Frutex ut videtur habitu variabili ut in *S. cordifolia;* ramuli novelli dense sericeo-villosi, hornotini

[9] Derived from ἀνάμεσος, intermediate.

pl.m. glabrescentes, autumno ut annotini vulgo partim pilosi, badii vel purpurascentes, etiam vetustiores saepe vix omnino glabri, dein nigro-purpurascentes vel epidermide secedente pl.m. cinereo flavescentes, ad circ. 5 mm. crassi. Gemmae ovato-oblongae, obtusiusculae, *initio dense pilosae, dein glabrescentes*, purpurascentes, petiolis duplo breviores. Folia adulta ut videtur papyracea, elliptica, elliptico-oblonga, ovali-elliptica vel elliptico-obovata, minima *interdum anguste elliptico-lanceolata vel oblanceolata*, margine integerrima vel rarius parva dentibus minimis sparsis glandulosis sub pilis occultis instructa (in no. 156 etiam majora distinctius sparse denticulata), *maxima nondum perfecte evoluta ramulorum* typi ad 2.5:1 cm. magna, in speciminibus a cl. Hartz in Augusto lectis ad 3.5:1.5 cm. magna et in ramulo vegeto (in no. 156) ad 4.8:2.3 cm. vel in forma satis incerta a Disco Island ad 5:2 cm. magna, superne ut videtur obscure viridia, in sicco vulgo pl.m. *nigricantia, novella inferiora adpresse sericea*, superiora pl.m. (praesertim versus marginem) villosula, adulta satis glabrescentia sed in costa pl.m. pilosula et margine ciliato-villosa, in epidermide pl.m. (saltem secundum nervos) *stomatifera, subtus valde discoloria*, glaucescentia, inferiora et novella dense sericea vel sericeo-villosa (pilis adpressis albis vel paullo flavescentibus), demum glabriora et adulta interdum tantum sparse pilosa, costa nervisque lateralibus 6–10 prominulis flavescentibus et laxe tenuiter reticulata. Petioli *initio dense, dein sparse sericeo-villosi, superne sulcati*, 2–5(–6) mm. longi. Stipulae breviter ovatae vel ovato-lanceolatae, acutae, denticulatae, ut folia colorata et pilosa, 1–3 mm. longa vel nulla (punctiformia). Amenta coetanea, ramulos breves *dense sericeo*-villosos foliatos sub anthesi vix ultra 12 mm. longos terminantia, *cylindrica, rhachide sericeo-villosa*; mascula 1.2–3:1 cm. magna, basi saepe sublaxiflora; bracteae oblongae, obtusae vel subobtusae, stramineae vel apice paullo fuscescentes, omnino sericeo-villosae et *apice magis sericeae; stamina 2, filamenta libera, circ.* $\frac{1}{3}$ *pilosa*, bracteis dein duplo longiora; antherae ellipsoideae, mediocres, violaceae (tantum juvenilia?), glandulae 2, ventralis anguste conica, apice truncata, integra vel pl.m. bipartita, dorsalis minor, angustior; feminea 1–2:0.8–0.9 cm., fructifera ut videtur ad 4:1.5 cm. (*Hartz, Holstenborg*) magna, *basi vix distincte laxiflora*; bracteae ut in masculis, saepe brevius pilosae, omnino stramineae;

ovaria ovoideo-oblonga, dense albo-villoso-tomentosa, subsessilia; styli distincti, bifidi vel bipartiti (brachiis saepe divaricatis) stigmatibus brevibus oblongis bifidis haud vel ad duplo breviores; *glandula 1, ventralis, ut in masculis, bractea circ. duplo brevior.* Fructus ovoideo-conici, ut videtur ad 8–9 mm. longi, minus dense quam ovaria villosi, subsessiles.

TYPE LOCALITY: *South Greenland, Ilua, lat. bor. 59°55′.*

RANGE: Southern and western Greenland.

SPECIMENS EXAMINED: Greenland: Ilua, lat. bor. 59°55′, May 15–31, 1889, *E. L. Lundholm* (m., f., type; M.); Sermiliarsuk, circ. 61°30′, August 3, 1889, *N. Hartz* (fr.; N.); Kingua Kuanersok, circ. 62°, July 12, 1889, *N. Hartz* (m.; N.); Kvanefjord S. f. Frederickshaab, 1886, *L. K. Rosenvinge* (no. 18873 O., fr.; needs further observation); Godthaabs district, Kobbefjord, June 28, 1884, *Warming* and *Holm* (m., f.; G.); Holstenborg, June 14, 1889, *N. Hartz* (f., fr. adult.; N.); Disco Island, Godthaab (probably mistake for Godthavn!), July 14, 1892, *W. E. Meehan* (no. 62 or 24768 O., m.; ramulis magis glabrescentibus annotinis fere glabris lucido-purpureis, forma porro observanda); Godthavn, August 2, 1896, *Cornell Party* (m., f.; Cor.; forma ut videtur prostrata aspectu *S. anglorum* non absimilis sed characteribus florum ab *S. anamesa typica* non diversa); Nugsuak Peninsula, Camp 2, August 10, 1896, *Cornell Party* (fr.; Cor.; forma porro observanda, bracteis magis obovatis, fructibus breviter pedicellatis, foliis apice saepe subito breviter plicato-acuminatis); Wilcox Head, August 15, 1896, *Cornell Party* (f., fr.; Cor.; forma porro observanda, amentis fructiferis ad 4.5:1.4 cm. magnis, fructibus pedicello quam glandula vix breviore suffultis, foliis ad 4:2 cm. magnis pl. m. obovato-ellipticis); Camp 3, August 20, 1896, *Cornell Party* (f.; Cor.; forma foliis satis breviter petiolatis ceterum paullo ad *S. anglorum* accedens); Upernivik, 72°47′, July 18, 1886, *L. K. Rosenvinge* (no. 24514 O., f.; looks very much like *S. cordifolia* but the pubescence reminds more of *S. anglorum;* on July 24 the same collector found a specimen at Pröven which I cannot distinguish from *S. anglorum*); Cape York, July 23, 1894, *E. H. Wetherill* (no. 214; G.; specimen mancum dubium tantum amentis fructiferis adultis praeditum habitu valde ad *S. anglorum* spectans sed bracteis breviter villosis oblongis); Omenak (Umanak) Fjord, Omenak Island, August 9, 1897, *D. White* and *Ch. Schuchert* (no. 156, fr.; N.; forma porro observanda, foliis ad 4.5:2 magnis, amentis fructiferis ad 3.5 cm. longis et 1.6 cm. crassis).

As already said, this species is certainly most closely related to *S. cordifolia*, from which it chiefly differs by the presence of stomata in the upper leaf surface. I should have treated it as a variety of this species were it not for the fact that there are a number of quasi intermediate forms between it and *S. anglorum*. On the other

hand, *S. anamesa* is not identical with *S. Waghornei*, which I take for a hybrid between *S. anglorum* and *S. cordifolia*. I have not yet seen any *S. anglorum* south of Disco Island in Greenland, and the Greenland material which I am inclined to refer to *S. cordifolia* is very scanty and needs further observation. From *S. anglorum* the new species may at once be distinguished by its hairy filaments and its narrowly oblong, light brown bracts, which have the rather short and villous pubescence of the *cordifolia* type. It seems to me that *S. anamesa* represents the plant commonly called *S. glauca* by LANGE, HARTZ, and other authors, but I am not sufficiently acquainted with the *Salix* of Greenland, owing to the scarcity of material from there in American herbaria, to give a more proper definition of the so-called *S. glauca* and the numerous varieties of it described by ANDERSSON, LANGE, and others. I do not find in the existing literature a name I could apply to *S. anamesa*. The *Salix* of Greenland seem always to have been compared only with those of Europe, while in fact the material before me indicates a much closer relationship with the species from Northeastern America. If we glance at the varieties of *S. glauca* mentioned from Greenland, we find the following in LANGE's Consp. Fl. Groenland. **1**:110. 1880, and **2**:279. 1887:

S. glauca var. *sericea* And., the type of which is *S. sericea* Vill., Hist. Pl. Dauph. **1**:382. 1786, nom. nud.; **3**:782. *pl. 51. fig. 27.* 1789, and which ANDERSSON refers to his f. 3. *lanceolata*. According to LANGE (1880) this var. *sericea* and also var. *appendiculata* (Vahl) Wahlb. are "tolerably common on some moist places." The latter variety is well figured by VAHL, Fl. Dan. 6. fasc. **18**:6. *pl. 1056.* 1792. Neither of these varieties seems to me identical with the forms I refer to *S. anamesa*. LANGE's third variety, var. *ovalifolia* Lge., Fl. Dan. 17, fasc. **50**:11. *pl. 2981.* 1880 (*S. glauca* α *sericea* 2 *ovalifolia* And.; ?*S. glauca* var. Brown in Trans. Bot. Soc. Edinbgh. **9**:450. 1868) pro parte, may be represented by the following 2 specimens before me: Disco Island, September 1854, *Lyall* (fr.; N., ex Herb. Hook.), and "Gebiet des Umanakfjordes (70–71° N.Br.)," August 18, 1892, *E. Vanhöffen* (no. 89[220], fr.; N.). The broad-elliptic or oval leaves which measure up to 3.5:2.3 or 5:2.2 cm., and are more or less villous, especially on the rib of the

upper surface and on the margin, do not have stomata in the upper epidermis, and their villous petioles are hardly 5 mm. long. Some of the leaves, especially in no. 89, show a few fine distant teeth toward the base. The branchlets of the season are covered with rather long villous hairs, while the older ones become glabrous and of a shining dark purplish color. The fruiting aments measure up to 4.5 by 1.5 cm., and the capsules are about 10 mm. long, including the very short pedicels. The habit of the plant cannot clearly be recognized, but there is another very similar fruiting specimen collected by *H. E. Wetherill*, at Netiulene, Whale Sound, North Greenland, August 13, 1894 (no. 226; G.), which certainly is taken from a prostrate plant. This number is enumerated by RYDBERG (1899) under *S. anglorum*, but it lacks the stomata in the upper epidermis, and seems more closely connected with the var. *ovalifolia*, being however a little more glabrescent than the other 2 specimens mentioned. The sessile capsules are about 8 mm. long, and the bracts somewhat darker.

The var. *angustifolia* Lange, Fl. Dan. 17. fasc. **50**:11. *pl. 2982*. 1880, is a very striking narrow-leaved form, the type of which came from Iceland ("prope Myvatu Islandiae legit cl. Lundgren"). I much doubt if it is the same as *S. glauca α sericea* 4 *angustifolia* And. (1868). LANGE (Consp. Fl. Gr. **1**:110) refers to it specimens from western and eastern Greenland which I have had no opportunity to compare. The only specimen I saw which somewhat resembles LANGE'S plate is *Wetherill's* no. 225 from the north side of the Jones Sound, August 1894 (f.; G.), but here the leaves have stomata in the upper epidermis and the rather silky pubescence of the dark bracts points more to *S. anglorum*, of which it may be a narrow-leaved form. I have seen rather similar specimens of *S. anglorum* from southwestern Victoria Land (*R. M. Anderson*) and northeastern Greenland (*A. Lundager*).

LANGE'S last var. *alpina* (not *S. glauca δ alpina* And., which is the same as *S. glauca β macrocarpa* Ledeb.) is described as a "fruticulus humilis, repens vel prostratus, ramis adscendentibus, foliis minutis, raro ultra ½ poll. longis," and as the type there has to be taken a specimen collected by *R. Brown* (of Campster) in 1867 at Jakobshavn in western Greenland (*S. glauca* Brown in Trans. Bot.

Soc. Edinbgh **9**:430. 1868, pro parte). I have seen nothing identical with this variety; there is only one specimen before me from the "Kvanefjord S. f. Frederickshaab," collected in 1886 by *L. K. Rosenvinge* (no. 18873 O., fr.) which I should take for a small-leaved form of *S. anamesa*, the narrowly elliptical leaves measuring up to 21:9 mm.

I can only repeat that we have to make a much closer investigation of the so-called *S. glauca* of Greenland in order to decide which of the forms can really be referred to the European species. They are certainly not identical with the var. *acutifolia* and var. *glabrescens* previously mentioned. I strongly believe that the true *S. glauca* is entirely absent from Eastern North America, and here represented by *S. cordifolia* and its varieties. It is the main purpose of these explanations to call attention to what is still unknown of the difficult forms of this group of willows, of which the following remains to be discussed.

10. S. LINGULATA Andersson in DC. Prodr. **16**^{2}:281. 1868; Herder in Act. Hort. Bot. Petrop. **11**:437. 1891.—This is a very poorly known Alaskan species not mentioned by COVILLE. ANDERSSON described it from specimens collected by *Kostalsky* "ad Alaxa" as a low shrub resembling in habit a small *S. arbuscula*. There are a few fragments in herb. N. ex Herb. Fischer which agree well with ANDERSSON's description (except that the leaves are not quite glabrous above), but are much too scanty to give a distinct impression of this species. The flowers, etc., suggest those of *S. desertorum*, and *S. lingulata* is certainly closely connected with the species of the GLAUCAE with pilose filaments, but has nothing in common with *S. reticulata*, to which it is said by ANDERSSON "capsulis globoso-ovalibus . . . . sat evidenter referrens."

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

THE SPORANGIA OF THISMIA AMERICANA

NORMA E. PFEIFFER

(WITH PLATE XVI)

Of the investigations among Burmanniaceae, the morphological studies of TREUB, JOHOW, and ERNST and BERNARD are prominent. These studies included both chlorophyllous and dependent forms, although the latter are better represented. The accounts vary considerably in completeness, since in the earlier ones close stages are sometimes lacking.

That there is variety within the family in development up to the mature seed is evidenced in the widely different accounts for those forms in which there is no evidence of fertilization, as compared with those where this process undoubtedly occurs. The net product seems to be approximately the same, that is, a small mass of endosperm cells about an embryo of from 2–10 or more cells, usually with no differentiation. A striking exception occurs in *Thismia clandestina*, which has a 3-celled suspensor and a spherical body differentiated into 2 layers. As in Orchidaceae (**12**), however, the preliminaries to this vary. Division of the megaspore mother cell may produce a row of 2 cells (as *Burmannia candida*, **5**), in which the inner cell gives rise to the embryo sac; or a row of 3 cells, the innermost of which, a true megaspore, functions in producing the female gametophyte; or the usual tetrad of angiosperms, of which the innermost megaspore is functional.

In the production of these cells the mother cell may go through a reduction division (as *Burmannia Championii*, **5**), in which case fertilization is the rule; or it may divide by an ordinary mitotic division, so that the progeny have the double number of chromosomes rather than the reduced number (*Burmannia coelestis*, **2**).

In all cases the embryo sac mother cell, whether a megaspore or the result of a single division of the archesporial cell, develops by 3 consecutive divisions to produce the 8-celled stage. Polarity is early evident, and the egg apparatus is organized, with small

antipodal cells at the opposite end of the sac, while the 2 polar nuclei usually meet near the center, sometimes nearer the chalazal or micropylar end (as *Burmannia Championii*, **5**).

When the egg is mature, in some cases there is evidence of the entrance of a pollen tube with the discharge of two male cells, one of which fuses with the egg, the other with the polar nuclei, as *B. candida*. That the latter fusion is not a complete one is held by ERNST and BERNARD, who see in a 3-parted nucleus with 3 nucleoli evidence against entire merging, at least in the first divisions of this endosperm nucleus. The fusion of the egg nucleus, however, is slower here than that of the 3 nuclei in the center of the sac. When there are 2–4 cells in the endosperm, the sex nuclei still remain distinct in *B. candida* (**5**). Later the fertilized egg gives rise to an embryo of 2 or more cells, varying with the form studied.

In cases where no fertilization has been observed there was development of seeds as indicated, except that no fusion save that of the polar nuclei occurred. *Thismia javanica* (**3**) and *Burmannia coelestis* (**2**), examples in which this condition holds, show no reduction division in the formation of the "megaspore." This condition is the one to be expected from such work as has been done in parthenogenetic angiosperms. The development of the seed is first evidenced in *B. coelestis* by the division of the endosperm nucleus, which usually results from the fusion of 2 polar nuclei; occasionally there are more than the two concerned, as 3–5, probably through the functioning of synergids or antipodal cells. Thereafter the development seems much as in sacs where fertilization has taken place. ERNST and BERNARD in their series of studies of Burmanniaceae report for *B. coelestis*, *B. candida*, *B. Championii*, *Thismia clandestina*, *T. Versteegii*, and *T. javanica*, practically the same sort of development in the endosperm region, regardless of the introduction of a male cell. The first division of the fusion nucleus gives rise to 2 nuclei, the lower of which is cut off by a wall. The cell thus formed is designated as the "basal apparat" or haustorium cell. The other nucleus, however, continues to go through successive divisions in which no cell plate is formed, with the result that there are a number of free nuclei in the endosperm region. Walls then develop in this region at approximately the same time or a

little before the beginning of nuclear division in the embryo cell proper. The extent of tissue development in *B. Championii* may be judged by ERNST and BERNARD's statement that there are 6–8 cells in the median longitudinal line in the mature sac, and that *B. coelestis* has about 30 endosperm cells at maturity.

The antipodal cells, never conspicuous, usually appear in a little V-shaped region below the haustorium region, sometimes as a row of cells, more frequently as two cells above one.

The cell giving rise to the embryo, whether after fertilization or not, goes through at least one nuclear division, and usually more. *Gonyanthes candida*, as reported by TREUB (13), develops a 2-celled embryo; as reported by JOHOW, and again by ERNST and BERNARD (as *B. candida*), it has a 3-celled embryo. JOHOW (8) found in *Gymnosiphon tenellus* a 3-celled situation similar to B. *candida*, and in *Dictyostegia orobanchioides* and *Apteria setacea* a 4-celled embryo, comparable to that found in *B. javanica* by TREUB (13). *Gymnosiphon trinitatis* (8) and *Thismia javanica* (3) show slightly greater development in a 6 or more-celled embryo, whereas *Thismia clandestina* (4) shows the greatest differentiation in a structure consisting of a 3-celled suspensor and a spherical body in which a single outermost layer of cells is differentiated from the inner mass. There is a striking similarity to Orchidaceae (12) so far as extent of development of the embryo is concerned. The contrast in the mature seed, on the other hand, due to failure of endosperm development in Orchidaceae, is equally noticeable. JOHOW, and later ERNST and BERNARD, have described the development of a small "nucellus polster" above the embryo sac, and an even more conspicuous tissue at the chalazal end. The possibility of the functioning of the latter at the time of germination of the seed as a region of water transfer (the rest of the tissue shows great cutinization) has been suggested, although no evidence of experimental character has been forthcoming. In contrast to the striking nucellus tissue at the ends, there is very evident degeneration of the cells in the middle zone or ring, as in *Gymnosiphon*, *Burmannia candida*, and *Thismia clandestina*.

In comparison with the thorough work done on embryo sacs, the scant attention paid to the pollen situation brings forth prac-

tically only the method of pollination and fertilization where this process occurs. This has been reported by several workers: MIERS (9) in *Dictyostegia orobanchioides*, WARMING on Brazilian forms and in *Apteria lilacina*, and ERNST and BERNARD in *Burmannia candida* and *B. Championii*. In all these forms germination of pollen occurs in the pollen sacs, so that the tufts or bundles of pollen tubes issue from the anthers and penetrate the stigma. MIERS remarked that the identity of these pollen tubes is clear with the use of a common lens, while the cottony mass of threads is evident, supposedly to the naked eye. He distinctly stated that this is not true, however, in *Myostoma* and *Ophiomeris* (9), and took this as evidence, in his early time, that thereby "the theory of the application of pollen tubes for the fertilization of its ovules is distinctly disproved." ERNST and BERNARD were unable to discover this method of pollination in *Thismia javanica* or *T. clandestina*, although aware of its presence in other forms and so alert for indications here. So far the evidence goes to show that such early germination of pollen and subsequent growth occur only in Euburmanniae, where the structure of the flower is different from that in *Thismia*. There seems to be a general conclusion, however, that forms are self-pollinated, through evidence such as given by SCHLECHTER in *Thismia Winkleri* (1, 11), where little diptera were found in the base of the flower where the pollen must fall.

Investigation

The material upon which the present study is based is that of *Thismia americana*, collected by the writer in Chicago, Illinois, during the summers of 1913 and 1914. The relationships of this form and a description of its structure, etc., were given in a previous paper (10).

In very young stages the stamen set appears to be distinct earlier than the ovary parts. Each stamen, of which there are 6, produces the usual 4 microsporangia, all of which are directed away from the central axis of the flower. Thus the surface of the anther toward the center is quite flat or slightly concave, while the opposite one is marked by the 4 lobes, in 2 pairs, which represent the rudiments of the microsporangia. At this stage usually the

connectives have not become so broadened as later, so that the individual stamens appear more distinct than the tube shows at maturity. The youngest stage where differentiation appears is indicated in fig. 14, where hypodermal masses of meristematic cells, separated from each other by a double layer of sterile cells, appear beneath a distinct, large-celled epidermal layer. At this time the ovary chamber is just beginning to show distinctly with the 3 placentae, which later give rise to the ovules projecting inward. Later the individual sporangia show the parietal layer to be but 2 layers thick, within which there is a conspicuous tapetum, while outside of it is the epidermal layer (fig. 15). The tapetum shows dark irregular bodies which may represent waste or reserve material. At this stage it is evident in many preparations that not all of the tissue originally differentiated as "sporogenous" is fertile. A number of the spores abort, so that in any one section only a few appear normal (fig. 16). Often between adjacent cells small oil globules appear as extraneous matter, possibly released through changes due to degeneration of the spores.

The microspores are shed from the stamens through a longitudinal dehiscence of the anther. At the time of shedding one division of the microspore nucleus has taken place in such as appear functional. The tube and generative nuclei can be distinguished quite readily, although often other bits of dark staining material are present.

Germination of pollen grains with formation of fine pollen tubes has been observed. By dissection of the style several tubes were traced through to the ovary cavity. At this time practically all the pollen had been shed from the stamens of the flowers under consideration. It seems likely that there is self-pollination as in other forms. The contrast with the Euburmannia forms reported lies in failure of development of the mass of pollen tubes from the microsporangia to the stigma, as reported by MIERS and ERNST and BERNARD. The structure would practically bar such a possibility, since the greatly developed stamen tube arising from the connectives usually extends below the level of the stigma. The dehiscence of the microsporangia occurs on the face away from the central region in which the style is erected, and the pollen falling from the

sacs would naturally drop to the floor of the cavity, that is, the roof of the ovary. In this fall it is obvious that the grains cannot come in contact with the stigma, which is separated by the stamen tube, although grains have been observed along the style. The cells of the inner surface of the stamen tube are often glandular in nature (fig. 16), although this would seem to have no special significance except in connection with the entrance of insects. It seems likely that the latter are necessary agents in pollination because of the mechanics involved.

The placentae which appear in the ovary during the development of the microsporangia give rise after a time to the primordia of the ovules (fig. 1). The surface of the placentae first becomes uneven through the appearance of the little lobes marking the rudiments. Soon the inner integument appears, and finally, as the ovule assumes the anatropous orientation, the outer integument is quite distinct except on the side where the funiculus appears. Meanwhile the hypodermal archesporial cell has become differentiated (fig. 2). The condition of mother cells usually occurs in the stamens at the same time that this archesporium appears in the ovule (cf. figs. 2 and 15). This cell represents the megaspore mother cell directly, since no parietal cells are developed here. It enlarges noticeably, and at length undergoes nuclear division, during which the chromatic material becomes massed at one side of the nucleus in synapsis (fig. 2). After division two cells separated by a thin wall are evident (fig. 3). At the same time the whole ovule is developing rapidly, as shown by the spindles in the tissue about the megaspore mother cell or its progeny. The two daughter cells divide further. The spindle in the outermost cell is oriented at right angles to the long axis of the ovule, that of the inner parallel to this axis. The result is that there is a pair of megaspores side by side which frequently are so crushed together in later stages that they lie obliquely (fig. 5) or appear finally as one (fig. 10). Sooner or later these cells disorganize, as does the sister cell of the functional megaspore, which lies innermost in the series of four. The pressure of development usually shows first on the outermost megaspores (fig. 5), but sometimes the third non-functional one is crushed first (fig. 6).

At the time of the first division of the megaspore developing the gametophyte, the abortive cells are dark staining, often wholly disintegrated masses of material. The binucleate stage shows nothing unusual, with its tendency toward polarity with the appearance of a central vacuole (figs. 8, 9). This stage is followed by the usual 4-nucleate situation arising from the division of each of the nuclei (fig. 10). The 4-nucleate phase must give rise very soon after formation to the 8-nucleate, since it represents a difficult stage to find.

The early 8-nucleate stages (fig. 11) show 4 free nuclei at each pole, with a large central vacuole. This is followed by great enlargement and the organization into an embryo sac of the typical form of angiosperms, the egg apparatus at the micropylar end consisting of 2 large synergids in contact with the egg, 3 smaller free antipodal nuclei in the narrower, more pointed chalazal end of the sac, and 2 polar nuclei, usually coming in contact with each other near the micropylar rather than the chalazal end (12). Stages both before and after the fusion of these polar nuclei have been found. The peculiar lobed effect reported by ERNST and BERNARD in *Burmannia candida* and interpreted there as incomplete fusion is sometimes evident here. That there is any special significance here seems doubtful.

At this time the cells surrounding the embryo sac stain more deeply and stand out more sharply than in younger stages. So far fertilization stages have not been observed. Contrary to ERNST'S report of development in *Burmannia coelestis*, it seems altogether likely that fertilization does occur, since pollen tubes are developed.

The development of the seed has not been followed in detail. At one time the larger portion of the sac is filled with the free nuclei resulting from the division of the endosperm nucleus. Soon walls come in, forming large cells. At about this time the egg cell undergoes division, so that a 2-celled proembryo is present imbedded in the conspicuous endosperm tissue. Further division occurs in the proembryo cells, and in the oldest material obtained (presumably mature seeds, although not so proved by germination) the embryo consists of many cells in a globular mass with a short suspensor region (fig. 13). The situation is much like that in

Thismia clandestina. The endosperm is packed with reserve material at this time, and stains very deeply as a result.

The development of the nucellus and integument into peculiar layers has been noted under the literature of other forms. In *Thismia americana* there is also at maturity a distinct mass of irregular small cells at the base connecting by means of a dark staining nucellar layer with a cap of peculiar cells at the micropylar end. The nucellar layer next to the endosperm shows fungal hyphae and many oil bodies as part of the contents. Gelatinization of the walls at the chalazal end begins early, and is responsible to some extent for the prominence of the mass of cells at that end.

Enough material has not been available to try a satisfactorily large range of germination experiments. Those which have been tested have given negative results. In all probability, as in orchids, the fungus plays a rôle in the early development of the plant.

Summary

1. In the microsporangia the sporogenous cells develop from hypodermal masses, 4 in number, in the usual fashion.

2. At maturity the innermost parietal layer appears crushed by the large tapetal cells.

3. There is marked abortion of sporogenous cells in the microsporangia.

4. The division of the megaspore mother cells gives rise to 4 megaspores, the outer 2 oriented at right angles to the long axis of the ovule.

5. The 3 outer megaspores degenerate very soon, disappearing entirely after a short time.

6. The functional megaspore divides in the usual way, so that eventually an embryo sac of 8 nuclei is produced.

7. Presence of pollen tubes makes fertilization seem likely.

8. The well developed embryo is imbedded in large endosperm cells which are conspicuous in storage contents.

9. In the seed the nucellus makes a conspicuous layer, developing into a cap of tissue at each end.

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EXPLANATION OF PLATE XVI

All figures were drawn with the aid of the camera lucida, and show magnifications as follows: figs. 1, 3, 5, 10, ×840; 13, 14, 15, 16, ×500; 17, ×260; 2, 7, 8, 9, 11, ×916; 4, 6, ×784; 12, ×1651.

FIG. 1.—Primordium of ovule.

FIG. 2.—Synapsis in megaspore mother cell.

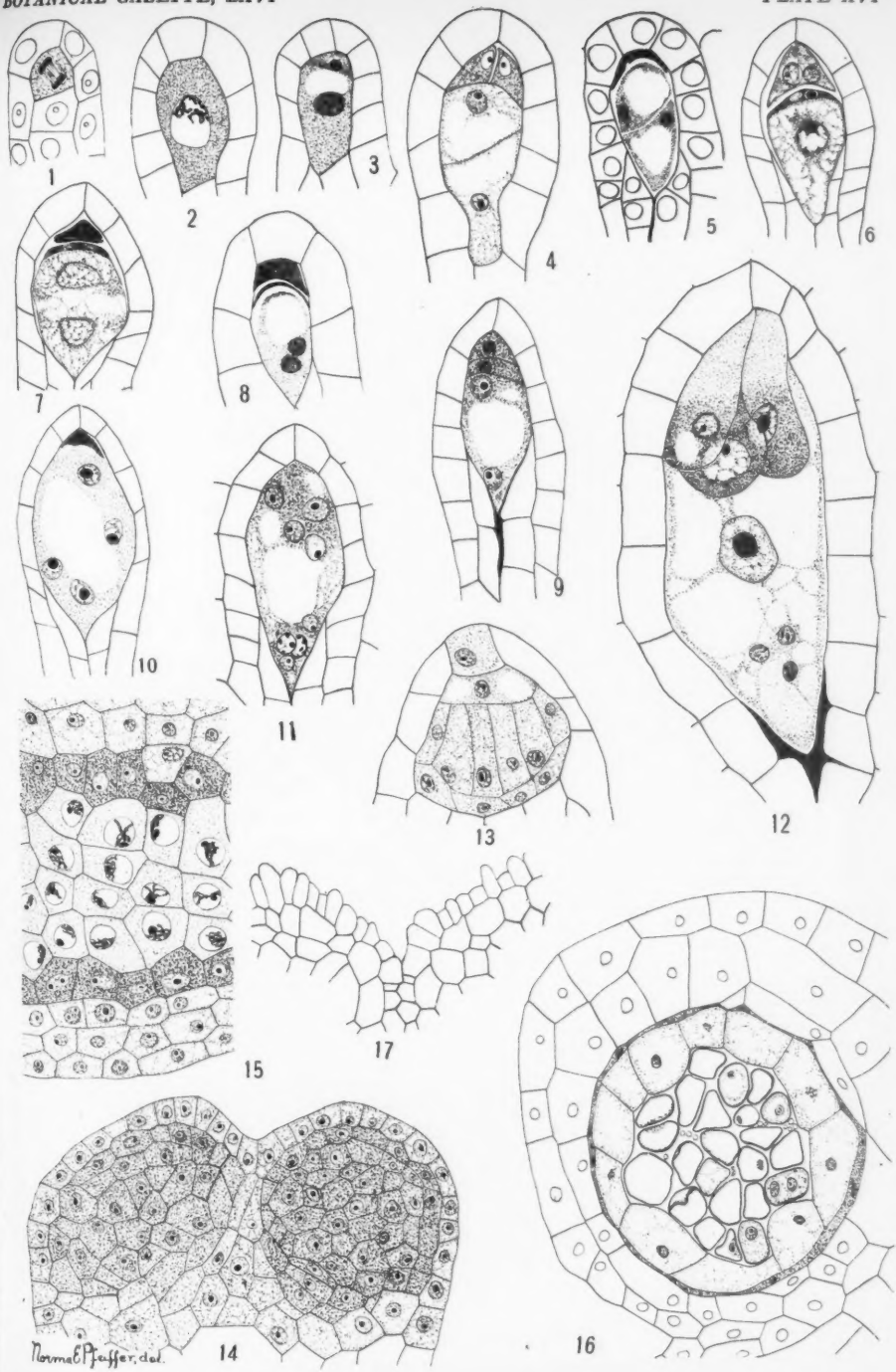
FIG. 3.—Daughter cells of megaspore mother cell.

FIG. 4.—Four megaspores.

FIG. 5.—Four megaspores, two outer cells already disorganized.

FIG. 6.—Same stage, but sister cell to functional megaspore crushed.

FIGS. 7–9.—Binucleate embryo sacs.



PFEIFFER on THISMIA

FIG. 10.—Four-nucleate embryo sac; non-functional megaspores disorganized.

FIG. 11.—Eight-nucleate embryo sac.

FIG. 12.—Embryo sac at maturity; chalazal walls conspicuously gelatinized.

FIG. 13.—Embryo.

FIG. 14.—Young anther, showing 2 of 4 microsporangia.

FIG. 15.—Microsporangium with mother cells in synapsis, longitudinal section.

FIG. 16.—Microsporangium, showing large number of sterile pollen grains, tapetum disorganizing.

FIG. 17.—Portion of stamen tube, showing glandular cells of inner surface (nearest style).

ROOT VARIATIONS INDUCED BY CARBON DIOXIDE GAS ADDITIONS TO SOIL[1]

H. A. NOYES, J. F. TROST, AND L. YODER

(WITH NINE FIGURES)

Under discussions of tropisms in plants it has been customary to include statements relative to the tropic influences of gases on plant roots. Primary investigations on this subject were made by MOLISCH,[2] using seedlings of *Pisum sativum* and *Zea Mays*. Gases were caused to flow past the roots of the plants, and tropic curvatures were reported for all the gases employed. BENNETT[3] repeated these experiments and concluded that the results obtained were hydrotropic. BENNETT made further studies with *Zea Mays*, *Raphanus sativus*, *Cucurbita Pepo*, *Pisum sativum*, and *Lupinus albus*, both in artificial and in so-called natural media. Studies made with the seedling roots in air gave no indication of aërotropism. Studies made in earth, when the sprouted seedlings were placed between blotting papers in pots of moist earth and then subjected to streams of carbon dioxide gas for periods varying from 24 to 60 hours, gave no definite curvatures.

CANNON and FREE,[4] after working with *Prosopis veluntia*, *Opuntia versicolor*, *Fouquieria*, *Coleus Blumei*, *Heliotropium peruvianum*, *Nerium oleander*, and *Salix* (probably *S. nigra*), concluded that "it seems probable that soil aëration must be added as a factor of no less importance than temperature and water," for these plants were found to have different responses to carbon dioxide added to soil. The following quotation is self-explanatory.

[1] Contribution from Research Chemistry and Bacteriology Laboratories of Department of Horticulture, Purdue University Agricultural Experiment Station, Lafayette, Indiana.

[2] MOLISCH, H., Über die Ablenkung der Wurzeln von ihrer normalen Wachthumsrichtung durch Gase (Aërotropismus). Sitzungsber. Akad. Wiss. Wien.

[3] BENNETT, MARY E., Are roots aërotropic? BOT. GAZ. **37**: 241–259. 1904.

[4] CANNON, W. A., and FREE, E. E., The ecological significance of soil aëration. Science N.S. **45**: 1917.

The ecological bearing of these facts is manifest. Although deficiency in aëration has frequently been suggested as an agricultural difficulty, or as the reason why certain species do not grow upon soils of heavy texture, it does not appear that this suggestion has had any exact experimental basis, nor does it seem to have been appreciated that different species may have great differences in the oxygen requirement of their roots and widely variant responses to differences in soil aëration, responses which appear to be quite as specific and significant as the responses to temperature and to available water which forms the present basis of ecological classification.

One of the writers[5] reported 2 preliminary experiments with *Zea Mays* and *Lycopersicum esculentum*. Flower pots containing these species were kept surrounded by an atmosphere of carbon dioxide. Practically all the aërial portions of the plants were in normal atmosphere. The plants responded differently to the gas during and subsequent to the 2 weeks' treatment given.

This paper is a report of experiments in which carbon dioxide gas was introduced subterraneously into soil in Wagner pots. Experiments will be reported following up the work of CANNON and FREE, in which the plants will be grown in soil sealed away from the air, so that there is no chance for the oxygen of the air to diffuse down into the soil. Studies on the effects of aëration on bacterial activities have convinced the writers that unless the soil worked with was sterile (which would be unnatural) or contained known organisms of known antagonisms and activities, the responses to changed conditions of aëration might be due to a cessation of certain necessary biological activities, or to the occurrence of certain detrimental biological activities. Adding carbon dioxide gas to the soil was expected to change the biochemical activities of the soil, but by having the atmosphere come in direct contact with the surface, it was believed that necessary biochemical activities could exist, although perhaps closer to the surface than normally. The surface of the soil of all pots was left normal (dust mulch), so that all conditions might more nearly approximate those present when the carbon dioxide content of the soil was increased by natural means. Differences in amount, nature, and type of root growth were thus to be attributed to the carbon

[5] NOYES, H. A., The effect on plant growth of saturating a soil with carbon dioxide. Science N.S. **40**: 1914.

dioxide gas added in equal amounts and in the same manner to all pots receiving gas treatments.

Equal weights of thoroughly mixed soil were put in paraffined Wagner pots of the most approved type (fig. 1). The soil in all pots was compacted by dropping each pot on the cement floor an equal number of times. Distilled water was added through the tubes to bring the moisture content up to one-half saturation, where it was kept by successive additions of water throughout the periods of investigation. The relative position of the pots was changed at regular intervals to correct differences in exposure and temperature in the greenhouse.

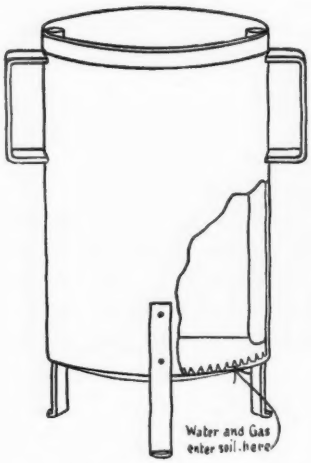


FIG. 1.—Wagner pot showing sub-irrigation tubes in place.

Experiment A

The Christmas pepper (*Capsicum annuum abbreviatum*) was the first plant used. Plants were started in November 1915 in the greenhouse from seed, and transplanted February 1 into the Wagner pots. The soil used was Sioux silt loam. The plants were about 1.5 inches high and carbon dioxide treatments were commenced after the plants became established. Three pots containing 4 plants each received no applications of carbon dioxide, 3 others received carbon dioxide applications 8 hours each day, and yet another set of 3 pots received carbon dioxide applications constantly. The gas was applied at the rate of approximately 650 cc. per hour, and fig. 2 shows the method of getting the gas from the pipe line to the individual pot. The wash bottles served as a means of equalizing the flow of gas into each pot. Fig. 2 shows the Christmas pepper plants after 4 months' treatment. At first the carbon dioxide treatment retarded growth, but by the time the picture was taken there was no great difference in size between the treated and untreated plants. Fig. 3

shows representative roots where no carbon dioxide gas was applied. The roots were uniformly long and fibrous and extended to the bottoms of the culture pots. Representative roots grown where the carbon dioxide treatment was 8 hours per day are shown in fig. 4. These roots did not penetrate to a depth lower than 7 inches. They were clumped and coarser when compared with those to which no carbon dioxide treatment was given. Aërial roots were quite prominent, and the main root was very thickly

FIG. 2.—*Capsicum annuum abbreviatum* 4 months after carbon dioxide gas treatments were started: row of pots fronted by no. 11 received constant carbon dioxide treatment; row fronted by no. 8 received 8 hours' carbon dioxide treatment daily; row fronted by no. 3 received no carbon dioxide treatment.

set with branching roots at a depth of about 3 inches. The roots shown in fig. 5 are representative of those that grew when the carbon dioxide treatment was constant. They compare unfavorably with those obtained under no treatment and under intermittent treatment. Aërial roots are many and prominent. The main roots are dwarfed and coarse and irregular. No roots were found at a depth lower than 5 inches. The carbon dioxide gas added to soil growing the Christmas pepper caused abnormal root developments. The gas had a much greater effect on the root development of the pepper plant than was apparent in the aërial portions.

The soil used for experiments B, C, and D was a fine sand, which has been classified by the Bureau of Soils as Wabash sandy loam. This soil was chosen because of its excellent physical condition and low organic matter content.

FIG. 3.—Representative roots of Christmas pepper plants which received no carbon dioxide gas treatments.

Experiment B

Head lettuce plants (*Lactuca sativa*) about 2.5 inches in diameter were transplanted into the pots in March 1917. Carbon dioxide treatments were started at once. Fig. 6 shows the best of each of the 3 triplicates. It is noted that carbon dioxide gas appears to have benefited the plants receiving treatment. These plants retained their relative sizes until harvested about 3 weeks later.

Fig. 7 shows the roots from the 2 most representative of each set of 3 plants grown under the different treatments. Carbon dioxide has affected the roots of these plants, although not to the extent that it did those of the Christmas peppers. Root devel-

FIG. 4.—Representative roots of Christmas pepper plants which received 8 hours' treatment of carbon dioxide daily.

opment departs from normal with increased carbon dioxide applications.

Experiment C

Radishes (*Raphanus sativus*) of the variety "Rapid Red" were sown in Wagner pots in March 1917. None of the plants were disturbed after the seed was sown. At the time of harvest the series of plants receiving no carbon dioxide gas applications had straight tap roots, while the roots of those receiving the gas showed

a perceptible tendency to horizontal growth. Large numbers of small roots were growing from the base of the bulbs in approximately horizontal directions. No photographs were taken of this experiment.

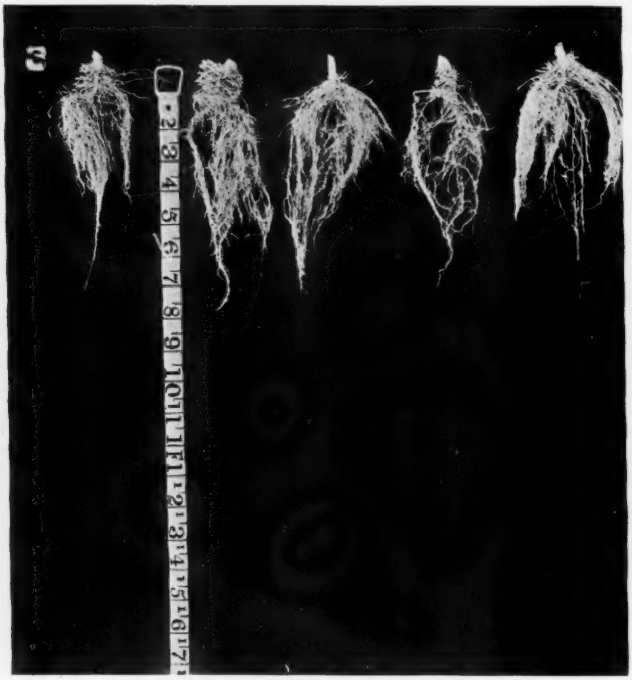


FIG. 5.—Representative roots of Christmas pepper plants which received constant treatment of carbon dioxide.

Experiment D

Burpee's stringless green pod bean (*Phaseolus vulgaris*) was grown from seed without and with the 2 carbon dioxide gas treatments. The plants were harvested just after blossoming ceased. Fig. 8 shows the plants growing in the best of each set of triplicate pots. The difference between the plants growing in the 3 pots is small. Fig. 9 shows the roots of the plants appearing in fig. 8.

Carbon dioxide gas additions to the soil did not prevent the roots from penetrating deeply, for in all pots the roots penetrated to the bottom. It was noted that roots grew to very near the openings

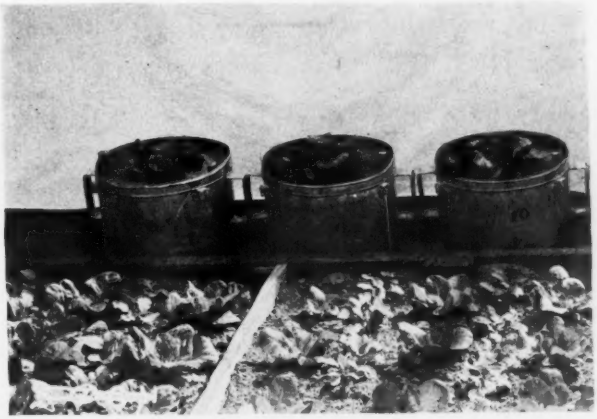


FIG. 6.—Best 3 *Lactuca sativa* of 9 under comparison: pot at left received no carbon dioxide, one in middle 8 hours daily, one at right constant treatment of carbon dioxide.

FIG. 7.—Representative roots of *Lactuca sativa:* 2 at left no carbon dioxide treatments, 2 in middle 8 hours' carbon dioxide treatment daily, 2 at right constant treatment with carbon dioxide.

where the carbon dioxide gas entered the pots. The gas had an effect on the development of the roots of the bean plant that was different from that observed with any other plant tested. The

intermittent carbon dioxide treatment was apparently about optimum for the development of the roots of this plant.

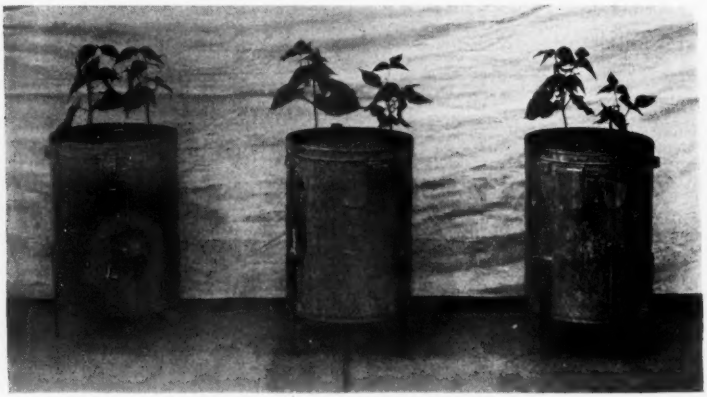


FIG. 8.—*Phaseolus vulgaris* subjected to different carbon dioxide treatments: pot at left received no carbon dioxide treatment, one in middle received 8 hours' treatment daily, one at right constant carbon dioxide treatment.

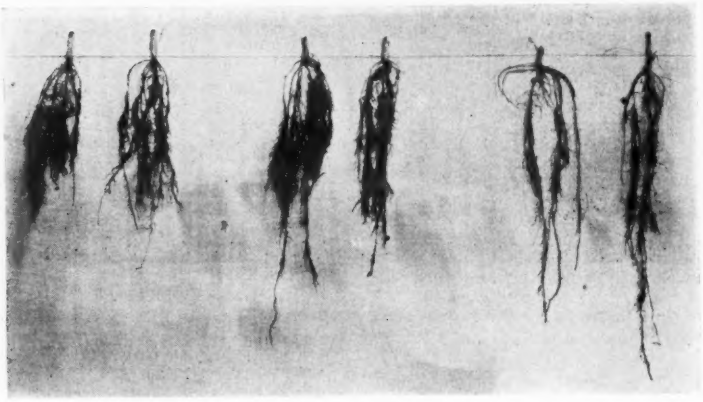


FIG. 9.—Roots of plants shown in fig. 8: 2 at left no carbon dioxide treatments, 2 in middle 8 hours' carbon dioxide treatment daily, and 2 at right constant carbon dioxide treatment.

Summary

1. Plants respond differently to carbon dioxide gas added to the soil in which they are grown.

2. The roots of the Christmas pepper, head lettuce, radish, and string bean were all found to be affected by additions of carbon dioxide gas to the soil.

3. The effects of carbon dioxide on root development were greater than those on the aërial portions of the plants.

4. The intermittent and constant applications of the carbon dioxide gas did not affect the roots of all the plants to the same extent.

5. The effect of the gas was not the same for the different plants used, although a constant treatment of 650 cc. of carbon dioxide gas per hour was apparently preventative of normal root development.

6. Decaying organic matter is held to be beneficial to growing plants. Cases have been cited by others where turning under immense amounts of green material has hurt the land temporarily; therefore the results obtained in these experiments lead to the belief that the carbon dioxide content of garden soils is sometimes detrimental to the root development of some plants growing in the garden.

7. The conclusion of CANNON and FREE that soil aëration must be a factor of no less importance in plant growth than water and temperature is supported.

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ABSORPTION OF SODIUM AND CALCIUM BY WHEAT SEEDLINGS[1]

HOWARD S. REED

(WITH ONE FIGURE)

Sea water, mammalian blood, and certain artificial solutions in which living cells are immersed are capable of continuing the life of those cells for considerable periods of time. These so-called "balanced solutions" may contain different ions which, separately, have a marked deleterious effect upon the cell, but which, when present in certain proportions, "balance" or "antagonize" each other. The result is that organisms live normally in such solutions.

There are two ways in which the mixture of ions or molecules in a balanced solution may overcome cytolytic factors: (1) by "antagonizing" each other, that is, by opposing and mutually excluding each other at the surface of the plasmatic bodies or other units of living structure; (2) by producing in the organism such a state of "tolerance," that is, by producing effects on the intracellular complexes, either alone or in conjunction with each other, that the harmful effects of single ions or molecules are eliminated. Or, in other words, the antagonism of ions may be either peripheral or internal.

Until recently the majority of physiologists were inclined to the former view, a view which was clearly stated in TRAUBE'S "sieve theory of permeability" and in OVERTON'S "lipoid-solubility" theory. Of the many objections to these two theories and to their various modifications, none was more cogent than that based on the fact that, even in a balanced solution, ions do slowly enter the cell. Indeed, if such were not the case, it would be impossible for the cell to obtain the salts necessary for its existence.

The objections to the former ideas of "antagonism" and "tolerance" have largely been met by a theory of antagonism pro-

[1] Paper 47, from the University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

posed by OSTERHOUT,[2] which holds that the slow penetration of salts may produce effects on the cell quite different from those produced by rapid penetration, and that their action is on the life processes rather than on the manner or rate of penetration. "From this point of view we regard the slow penetration of salts in balanced solutions not as the cause but as the result of antagonism, or rather we may regard the slow penetration and the increased length of life (or growth, etc.), by which we measure antagonism, as the results of certain life processes which are directly acted on by the antagonistic substances."

OSTERHOUT found that the theory was satisfactorily supported when the penetration of certain known mixtures of NaCl and $CaCl_2$ into living cells was studied. He makes, however, a seeming exception in the case of solutions of lower concentration, stating: "Below the saturation point[3] the relative proportions of the salts will be of less importance than their total concentration; this is the case at low concentrations in the region of the so-called 'nutritive effects.'"

SHIVE and TOTTINGHAM, on the other hand, not to mention others, have rather definitely shown that there are certain distinctly favorable ratios in nutrient solutions of equivalent concentration.

In view of OSTERHOUT's rather sweeping exclusion of nutrient solutions of low concentration, it seemed profitable to the writer to investigate the effect of some of OSTERHOUT's proportions in weak solutions, coupled with analyses of the plants to determine the amounts of solute taken up. It is a pleasure to acknowledge my indebtedness to Mr. J. F. BREAZEALE for the cultures and analyses upon which this work is based.

The experiments to be reported were conducted on wheat seedlings grown on disks of perforated aluminum buoyed by glass bulbs

[2] OSTERHOUT, W. J. V., The penetration of balanced solutions and the theory of antagonism. Science, N.S. **44**:395. 1916.

———, A dynamical theory of antagonism. Proc. Amer. Phil. Soc. **55**:533. 1916.

[3] The term "saturation point" as used is taken to mean the point at which the surface of a plasmatic structure is saturated with the antagonizing salts. Beyond this point an increase in their concentration in the solution produces no effect on their concentration in the surface.

in such a way that the aluminum disk floated at the surface of the solution. Each disk was floated on about 3 liters of solution in an agate enameled pan. The seeds were germinated in a solution of the same composition as that designed for the experiment. None but sprouted seeds were used. Each disk originally held about 1000 seedlings, but careful selection brought the number down to about 200.

In attempting to study the effect of a small amount of calcium, special precautions are necessary, owing to the abundance of calcium compounds in our environment. The seeds and apparatus used must be washed in dilute HCl and rinsed with distilled water of undoubted purity. The cultures must be carefully protected from dust, especially dust from plastered walls, or from cement floors, which might carry salts of calcium, since 1 part per million of calcium may produce distinct effects. It is necessary to work in somewhat the same way as one works with cultures of bacteria.

The antagonism of calcium and sodium has been a matter of record in connection with OSTERHOUT'S data. The case is illustrated by the cultures shown in fig. 1, which show the toxic action of 4000 p.p.m. NaCl and the antidoting action of $CaSO_4$, CaO, and $Mg(HCO_3)_2$. The wheat seedlings shown in the figure were similar at the outset and grew 7 days in the respective cultures. The concentration of 4000 p.p.m. NaCl is about the toxic limit for wheat seedlings under these conditions, yet 30 p.p.m. of a calcium salt antagonized completely the toxicity. Magnesium bicarbonate was not so successful in overcoming the bad effects of sodium chloride.

A further illustration of the antagonistic action of calcium is shown in table I, which gives data pertaining to wheat plants grown in solutions of sodium chloride with and without the addition of CaO. It will be seen that (1) measured by ash content and by dry weight of plants the addition of 30 p.p.m. CaO was beneficial to growth; (2) the amount of NaCl absorbed by the plants was not decreased when CaO was added. In the case of cultures 4 and 5 of table I the ratio of NaCl to total ash is 1:1.9 where only NaCl was present in the solution and 1:2.3 where both NaCl and CaO were present. From this it would seem that the calcium salt

has not benefited the plant by excluding sodium, especially in view of the amount found in the tops, but rather has rendered it harmless within the plant.

A second set of cultures was made in which the ratios of sodium to calcium were identical with some of those employed by OSTERHOUT. The pure NaCl and $CaCl_2$ solutions were each 0.004M.

FIG. 1.—Effect of calcium and magnesium salts upon toxicity of sodium chloride to wheat plants: culture solutions were jar 1, 4000 p.p.m. NaCl; jar 2, 4000 p.p.m. NaCl plus 30 p.p.m. $CaSO_4$; jar 3, 4000 p.p.m. NaCl plus 30 p.p.m. CaO; jar 4, 4000 p.p.m. NaCl plus 30 p.p.m. $Mg(HCO_3)_2$.

This is much less than the concentration of NaCl employed in the first series, being 230 p.p.m. of NaCl instead of 4000 p.p.m. This series of cultures was continued for 16 days, at which time 100 representative plants were withdrawn from each culture, weighed, and analyzed, giving the data shown in table II.

It seems quite evident from these results that one of the ratios of Na:Ca in which OSTERHOUT found the greatest amount of antagonism was the one most favorable for growth in this series.

TABLE I

EFFECT OF CALCIUM OXIDE ON GROWTH AND ABSORPTION OF SODIUM CHLORIDE BY WHEAT PLANTS

PLANTS GROWN IN	DAYS	ANALYSIS OF 100 TOPS		ANALYSIS OF 100 ENTIRE PLANTS				
		Ash	NaCl	Green weight	Dry weight	Ash	CaO	NaCl
1. Distilled water	8	0.0462	trace	.....	2.077	.....	.....	trace
2. 4000 p.p.m. NaCl	8	0.0775	0.0320	.....	1.993	.....	.....	0.0553
3. Same plus 30 p.p.m. CaO	8	0.0921	0.0334	.....	2.352	.....	.....	0.0595
4. 4000 p.p.m. NaCl	10	.....	.....	7.6	1.740	0.0940	0.0006	0.0485
5. Same plus 30 p.p.m. CaO	10	.....	.....	12.2	1.820	0.1240	0.0030	0.0543
6. Distilled water	8	.....	.....	.....	.....	0.0570	0.0026	.....
7. 4000 p.p.m. NaCl	8	.....	.....	.....	.....	0.0660	0.0009	.....
8. Same plus 30 p.p.m. CaO	8	.....	.....	.....	.....	0.0910	0.0017	.....

Plants grown in the solution containing 98Na:2Ca attained the greatest dry weight and were larger than any others in the series. From this solution the greatest amount of ash constituents was

TABLE II

WHEAT PLANTS GROWN 16 DAYS IN SOLUTION CULTURES; 100 PLANTS WITH SEEDS ATTACHED

RATIO OF NA AND CA IN SOLUTION	COMPOSITION OF 100 PLANTS				RATIO OF NA TO ASH
	Dry weight	Ash	Ca	Na	
1. 100Na: 0Ca	2.10	0.1950	0.006	0.017	1:11.5
2. 98Na: 2Ca	2.74	0.2250	0.0102	0.022	1:10.2
3. 85Na: 15Ca	2.37	0.1730	0.0106	0.019	1: 9.1
4. 65Na: 35Ca	2.41	0.1842	0.0132	0.016	1:11.5
5. 38Na: 62Ca	2.27	0.1930	0.0204	0.012	1:16.1
6. 0Na: 100Ca	2.33	0.2040	0.0226	0.008	1:25.5

absorbed and also the greatest amount of sodium. None of the other solutions appeared to contain as favorable a ratio of sodium to calcium, although the dry weight of plants in the last 4 solutions does not vary enough to offset the experimental error. The

Na:ash ratio in the first 4 sets of plants does not show any real difference. In the last 2 the relative amounts of sodium are less.

The amounts of sodium and calcium actually absorbed and retained by the plants may be of more interest to consider because they will show what the plants in the various cultures actually "fixed." The results shown in table III are taken from table II,

TABLE III

AMOUNTS OF Na AND Ca ABSORBED FROM SOLUTIONS BY WHEAT PLANTS IN 16 DAYS

RATIOS FURNISHED	AMOUNTS ABSORBED	
	Na	Ca
1. 100Na: 0Ca	0.009	0.000
2. 98Na: 2Ca	0.014	0.0042
3. 85Na: 15Ca	0.011	0.0046
4. 65Na: 35Ca	0.008	0.0072
5. 38Na: 62Ca	0.004	0.0144
6. 0Na: 100Ca	0.000	0.0166

and show the amounts of sodium and calcium after deducting what was found in plants grown in solutions containing none of the element in question.

These results show that the greatest amount of sodium was absorbed from the solution containing the ratio 98Na:2Ca. Less sodium was absorbed from any other combination, even from pure sodium chloride. At the same time they also show no such selective absorption in the case of calcium. The amounts of calcium absorbed increase steadily as the amount in the solution increases, reaching their maximum in pure calcium chloride. There appears to be a "preferred ratio" of calcium for sodium, but none of sodium for calcium, although more cultures employing smaller amounts of sodium chloride should have been tried.

Summary

The antagonism of calcium and sodium which has been found by other workers exists also in more dilute solutions and may be shown by chemical analyses of the plants grown therein.

Concentrations of sodium chloride which were strongly toxic to wheat seedlings were antidoted by 30 parts per million of calcium oxide.

The most successful antagonism in the concentrations employed was found when the Na:Ca ratio was 98:2. At this ratio the calcium was not found to exclude sodium from the plant, but to render it harmless after entrance. The antagonism appears to be internal rather than peripheral.

UNIVERSITY OF CALIFORNIA CITRUS EXPERIMENT STATION
RIVERSIDE, CAL.

BRIEFER ARTICLES

METHOD OF REPLACING PARAFFIN SOLVENT WITH PARAFFIN

Some years ago LAND[1] proposed a method of insuring the gradual saturation with paraffin of the xylol now almost universally used as the clearing medium and paraffin solvent in the paraffin method. He suggested the placing of a section of fine wire screening below the level of the xylol in the shell vial upon which the paraffin ordinarily grated into the vial would be held. Such an arrangement obviates the danger of allowing the paraffin fragments to fall to the bottom of the container, there to be in contact with the material and to surround it almost at once with a high percentage of dissolved paraffin.

For some years previous to the publication of LAND's suggestion in this matter we had been employing, in this laboratory, similar devices to insure the gradual saturation of the paraffin solvent. Some time ago, however, we replaced this method for most material with another which is more simple and has given consistently good results. In this scheme melted paraffin is carefully poured on the surface of the xylol in a shell vial until a plug of the desired thickness is formed. A hot needle run around the inside of the vial will loosen the plug of paraffin, which is then pushed down below the level of the xylol. We have never found an instance in which the paraffin plug slipped down to the bottom of the vial or indeed changed its original position appreciably.

The entire paraffin plug becomes rather rapidly saturated with xylol and a layer of xylol-paraffin soon forms at the lower surface of contact. If the vial is not shaken, a very gradual saturation of the xylol takes place, and at the end of 4–6 days the xylol has taken up its maximum quantity of paraffin. In practice we pour a plug of paraffin which will weigh 4–6 gr. into a vial containing 10–15 cc. of xylol.

The increase in time required according to this scheme in the paraffin method seems justified by the rather ideally slow replacing of the paraffin solvent by paraffin. It is often desirable to cool the vial containing the

[1] LAND, W. J. G., Microchemical methods, an improved method of replacing the paraffin solvent with paraffin. BOT. GAZ. **59**: 397. 1915.

xylol under the tap before pouring in the paraffin. The latter step requires only slight practice to be successful, and indeed the only effect of a too rapid pouring in of the melted paraffin seems to be the formation of strings of paraffin reaching down into the xylol. If the paraffin plug needs to be removed at any time, this can be accomplished readily by forcing through it a hot needle, the tip of which has been bent at right angles. The needle after cooling for an instant may be turned slightly and the plug pulled from the vial.—T. H. GOODSPEED, *University of California.*

ADAPTATION AND NATURAL SELECTION

I wish to correct a false impression which my paper on the agency of fire in the propagation of the longleaf pines (BOT. GAZ. **64**:497–508. 1917) has left in the minds of some of my correspondents, to whom it seems that the conclusions there reached might lead to the absurd economic paradox that forest fires should be encouraged for the conservation of our pine lumber supply. As a matter of fact, all the evidence produced in that paper was intended to show that it is their *adaptation for resistance* to fire which insures the survival of this species. The action of natural selection in this case, as in practically all others that have come under my observation, is negative and indirect. It preserves not by selection of the fit, but by elimination of the unfit, thus giving the best adapted a free hand in the struggle for existence.

In calling attention, therefore, to the peculiar relation between the longleaf pine and fire, there was no thought of suggesting that we should imitate the method of nature; but having learned that a clean forest floor and plenty of sunshine are essential conditions for the propagation of the longleaf pine, these conditions may be secured by other means than fire, such as judicious cutting and thinning, and a periodic cleaning up of the forest floor. Whether a well guarded ground fire at the proper season might not be a useful aid in accomplishing this last purpose is a question which must be left for the practical forester to decide.—E. F. ANDREWS, *Rome, Ga.*

CURRENT LITERATURE

MINOR NOTICES

Mosses and ferns.—A third edition of CAMPBELL'S well known textbook[1] has appeared. The body of the text is the same as in the second edition of 1905, the new material being added in the form of an appendix, under the corresponding chapter headings. In addition to numerous contributions by other investigators, the appendix contains noteworthy results of the author in his investigations of tropical liverworts and ferns. The bibliography is completely recast, including 772 titles, distributed among 336 authors. The author has rendered an important service to morphologists in bringing up to date, and in convenient form, our knowledge of these great groups.—*J. M. C.*

NOTES FOR STUDENTS

Mitochondria.—GUILLIERMOND has published a number of short reports dealing with the results of his investigations on the nature and function of mitochondria. In a paper[2] dealing with the origin of chromoplasts and pigments, he finds that chromoplasts are formed from mitochondria, more especially from the elongated forms called chondriocontes; and that pigments of the xanthophyll and carotin groups are elaborated either (1) directly by the mitochondria, or (2) by chromoplasts which arose from mitochondria, or (3) by chromoplasts resulting from a metamorphosis of chloroplasts which in turn arose from mitochondria. Added interest is given because of the fact that in a great many plants the process can be observed in the living material under the microscope. Both granular and crystalline pigments have the same origin. Epidermal cells from petals of *Iris germanica*, *Tulipa suaveolens*, *Tropaeolum majus*, and young fruits of *Arum maculatum*, *Asparagus officinalis*, and numerous others furnished the material for this study.

In a later paper[3] dealing with the chondrium of *Tulipa*, he reports that the mitochondria are easily visible in the living material under the oil immersion lens. Epidermal cells from petals are used. The mitochondria are long, thin, and undulate, although smaller granular and rod mitochondria are present. Material is at its best just about the time the flowers first open. The reviewer has verified these observations with the yellow-flowered variety, but was not

[1] CAMPBELL, D. H., The structure and development of mosses and ferns (Archegoniatae). 3d ed. 8vo. pp. 708. *figs. 322*. New York: Macmillan Co. 1918. $4.50.

[2] GUILLIERMOND, A., Compt. Rend. Acad. Sci. **164**:232–235. 1917.

[3] ———, *Loc. cit.* **164**:407–409. 1917.

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[2] GUILLIERMOND, A., Compt. Rend. Acad. Sci. **164**:232–235. 1917.

[3] ———, *Loc. cit.* **164**:407–409. 1917.

successful with the white ones, and found further that the mitochondria begin to disintegrate in the course of 30 minutes after the mount is made.

In a third paper[4] dealing with alterations of the chondrium, he finds that "the mitochondria are the most fragile elements of the cell, and it is through them that the first signs of degeneration and the first symptoms of trouble due to osmotic changes are manifested." The alteration consists of the transformation of the mitochondria into vesicles having the aspect of vacuoles and giving the cytoplasm an alveolar appearance. This, the author remarks, is interesting when we think of BÜTSCHLI's alveolar structures.

In a fourth paper[5] dealing with the fixation of cytoplasm, he finds that from the point of view of their action on the chondrium fixing agents may be grouped in three classes: (1) alcohol, Mann's, Zenker's, and Carnoy's fluids all disturb the structure of the cytoplasm and destroy the mitochondria; (2) picric acid, mercuric chloride, formalin, and strong Flemming's generally cause a pronounced shriveling of the mitochondria, often accompanied by a diminution of the chromaticity of these structures; (3) Altmann's, Benda's, Regaud's, and Flemming's with only a trace of acetic acid are the fixing agents commonly used for fixing mitochondria and the cytoplasm as nearly like living as possible. In general it is those reagents which contain alcohol or acetic acid which alter the mitochondria most.

MOTTIER[6] has published a valuable contribution to the study of mitochondria, not only in the new facts he has revealed, but more especially in the account of his methods, which will enable workers much less qualified to take up studies in this interesting field. In the main he used Flemming's fluid, with very much reduced amounts of acetic acid for a fixative and iron haematoxylin and crystal violet for stains. For material he used root tips of *Pisum sativum*, *Zea Mays*, and *Adiantum pedatum;* the thallus of *Marchantia polymorpha*, *Anthoceros*, and *Pallavacinia;* seedlings of *Pinus Banksiana;* leaves of *Elodea canadensis;* and certain algae.

He finds that root tips of *Pisum* furnish excellent material for a study of the primordia of plastids and their transformations. Mitochondria-like structures are very numerous, such as rods of various lengths and thicknesses, straight, variously curved and bent, and also numerous smaller granules and slender delicate rods. Leucoplasts develop from the larger structures, but the smaller ones do not form plastids. Although these structures all give the same histochemical reactions, the term chondriosome (mitochondrium) is reserved for those smaller structures which do not form plastids. The former he calls "plastid primordia." *Zea Mays* is similar in all essentials to *Pisum*. In *Marchantia* the "plastid primordia" are more readily distinguished from the

[4] GUILLERMOND, A., *Loc. cit.* **164**:609–612. 1917.

[5] ———, *Loc. cit.* **164**:643–646. 1917.

[6] MOTTIER, D. A., Chondriosomes and the primordia of chloroplasts and leucoplasts. Ann. Botany **32**:91–114. *pl. 1.* 1918.

mitochondria in that they are larger and rounded, while the mitochondria are very small granular or rod forms. Cells from the thallus of *Anthoceros* were studied because they have each a single chloroplast and hence furnish favorable objects for determining whether mitochondria are merely disorganized chloroplasts. This question is answered in the negative. In *Adiantum pedatum* he finds that the mitochondria are small, granular, and rod-shaped. Discussion is here confined to root tips, and we are promised a subsequent paper dealing with other parts. The "plastid primordia" are rounded, lenticular, and rod-shaped, but much larger than the mitochondria. The rod-shaped "primordia" which do not develop into leucoplasts "continue to elongate into long-drawn-out threads and finally disappear." In the younger growing parts of the stem of *Pinus Banksiana* numerous small rounded bodies with colorless centers (plastid primordia) and densely staining granules (mitochondria) were found. In the older parts these bodies with the colorless centers form the plastids, while the granular mitochondria have become larger or formed rod mitochondria. In the leaves of *Elodea canadensis* the primordia are rod-shaped and can easily be traced in their transformation into plastids. The mitochondria are very numerous, and in cells with fully developed chloroplasts they are globular and even rod-shaped, differing from the primordia only in size. We are promised a later paper dealing with his results on *Hydrodictyon*.

GUILLIERMOND includes under the term mitochondria all those structures which give the same histochemical reactions, regardless of their functions; while MOTTIER, on the other hand, considers only those structures which do not develop into plastids to be included under the term. Both, however, agree that these structures are "morphological units of the cell with the same rank as the nucleus." MOTTIER goes farther and asks, "What characteristics are transmitted solely by the nucleus, and what by the primordia of plastids and by the chondriosomes? There are many transmissible characteristics which cannot as yet be definitely expressed in any Mendelian ratio. To claim that certain phenomena of fluctuating variations and other numerous characteristics, Mendelian or otherwise, owe their appearance and transmission to the primordia of plastids and chondriosomes may be a daring hypothesis, but if, as there is good ground to believe, these bodies are permanent organs, there is no escape from some such assumption."—RAY C. FRIESNER.

Units of vegetation and their classification.—With the advance of the science of ecology there has been a gradual evolution of opinion as to the units most suitable for the analysis and study of vegetation. The earlier stages of this evolution have been well discussed by Moss,[7] who also advanced the developmental concept of the plant formation. The half decade following this paper passed without a further notable contribution to the subject, but recently three

[7] Moss, C. E., The fundamental units of vegetation. New Phytol. 9:18–53. 1910.

articles have appeared that are notable, not only for the divergence of the views expressed, but also for the decided advance they have made in providing a logical system of classified units for the use of students of vegetation.

GLEASON[8] embodies in his article an individualistic concept of ecology, contending that all phenomena of vegetation depend upon the phenomena of the individual plant. The plant association he conceives to be an area of uniform vegetation developed by similar environmental selection from the immigrants from the surrounding population. This position, while extreme, will prove most useful if it serves to focus attention upon the intensive study of some of the most important species of a vegetation so as to discover their reactions to various environments and to the factors which limit their invasion and establishment in plant communities.

The other extreme is seen in the work of CLEMENTS,[9] as expressed in what doubtless is the most notable of recent contributions to ecological literature. Without attempting to review or criticize his book as a whole, it may be pointed out that he selects the formation as the fundamental unit and regards this plant community as an organic entity exhibiting origin, growth, maturity, and death. As an organism it is able to reproduce itself and possesses a life history which is a complex but definite process. The climax community is the adult organism of which all initial and medial stages are but stages of development. Thus CLEMENTS would limit the term formation to the climax community, while the successional series leading up to the climax formation he calls a "sere." He has provided a complete system of subordinate units for the analysis of both formation and the sere, the former being divided successively into associations, consociations, societies, and clans; the latter into associes, consocies, socies, colonies, and families. This recognition of a plant community as an entity comparable in some extent at least to an organism seems strictly in accord with the views of most ecological workers, and if the relationship be regarded as one of close analogy rather than homology it will probably prove the most stimulating and satisfactory attitude. It appears, however, that CLEMENTS' system of subordinate units is rather more elaborate than is required to meet the needs of most investigators.

A somewhat simpler system, introducing but few new concepts or terms, recently organized by NICHOLS,[10] commends itself to the reviewer as including those units and terms which in the past have proved most satisfactory, and which now for the first time have been combined in a definite system. NICHOLS

[8] GLEASON, H. A., The structure and development of the plant association. Bull. Torr. Bot. Club **44**:463–481. 1917.

[9] CLEMENTS, F. E., Plant succession. Carn. Inst. Wash. Pub. 242. pp. xiii+511. *pls. 61*. 1916.

[10] NICHOLS, GEO. E., The interpretation and application of certain terms and concepts in the ecological classification of plant communities. Plant World **20**:305–319, 341–353. 1917.

himself claims that the scheme is the outgrowth of the classification originally presented by COWLES,[11] and by his selection of the association as the fundamental unit of vegetation he recognizes the tendency of ecologists as a whole to become more and more agreed upon the use of the term "plant association," even while differing somewhat as to the content of the term. He defines the association as any community of plants, taken in its entirety, which occupies a common habitat, or in other terms, any stage in a given successional series. The "habitat," thus made the criterion of the association, is understood to be a unit area with an essentially uniform environment made up of a complex of climatic, edaphic, and biotic factors which determine the ecological aspect of the vegetation. The subdivisions of the association agree with those of CLEMENTS in being consociation and society, but differ in that "association" (and its subdivisions) is applied to both the climax and the seral units.

Here NICHOLS has added a most useful although rather abstract concept of "association type," defined as "a type of plant association which is correlated with a given type of habitat." The association type which represents the highest degree of mesophytism which the climate of the region permits is regarded as the regional climax. It has been usual to regard as permanent only such associations as are included in such a regional climax type, but NICHOLS holds that in edaphically unfavorable situations not only is succession much slowed down, but that it often becomes permanently arrested at a point far short of the climax just mentioned. In this way there would be developed permanent associations less mesophytic than the regional climax association type. These may be distinguished as belonging to an "edaphic climax." Most ecologists recognizing this situation have preferred to regard such associations as belonging to a "temporary climax," postulating the eventual although much delayed dominance of a climax limited by climate only.

Grouping plant associations upon a developmental basis, the plant community of the next higher order is termed an "edaphic formation" and defined as "an association-complex which is related to a specific physiographic unit area." Here the "formation" differs from that of CLEMENTS in including not only the climax community but also those of seral rank. Edaphic formations are in turn grouped into "edaphic formation-types" and the "edaphic formation-complex" for any climatic region constitutes a "climatic formation." In this use of the terms edaphic formation and climatic formation NICHOLS has retained the well known classification of SCHIMPER, while modifying the concepts to include the developmental idea. The various climatic formations belong to various "climatic formation-types," several of which may form the "climatic formation-complex" of a continent or other large unit area.

NICHOLS has further demonstrated the utility of his excellent scheme of classification by applying it to the analysis of the vegetation of northern Cape

[11] COWLES, H. C., The physiographic ecology of Chicago and vicinity. BOT. GAZ. **31**:73–108, 145–235. 1901.

Breton Island, appending various explanatory remarks which should prove useful to students attempting to make similar applications to other regions.—GEO. D. FULLER.

Permeability.—Several interesting contributions to our knowledge of protoplasmic permeability have appeared recently. DELF[12] has investigated the influence of temperature on the permeability of protoplasm to water by the tissue shrinkage method, using sections of onion leaves and dandelion scapes in subtonic solutions of cane sugar. The curve of contraction at different temperatures was measured by means of an optical lever which greatly magnified the shrinkage, and from this curve the rate of contraction at the time when 30, 50, and 70 per cent of the shrinkage had occurred, was measured by the tangents to the curves at these points. From the rates the values for Q_{10} were obtained. This value increases as the temperature rises. In the onion leaf the value of Q^{10} at 10–20° C. is 1.5, at 20–30° C. is 2.6, and at 30–40° C. is 3.0. In the dandelion scape the greatest value of Q_{10} was obtained at 20–30° C., at which temperatures it was 3.8. Above and below those temperatures the value falls. Contrary to the results of VAN RYSSELBERGHE, who found very little increase in permeability above 20° C., DELF finds that permeability of the protoplasm to water continues to increase rapidly up to the highest temperature investigated, 42° C. The methods used by VAN RYSSELBERGHE are justly criticized, particularly with reference to the means of deriving a temperature relation from his data. The strength of solutions used by VAN RYSSELBERGHE may also have led to serious errors.

Miss HIND[13] has studied the absorption of acids by living plant tissues, using electrical conductivity methods, and electrometrical measurement of the H^+ ion concentration in acid solutions which were in contact with living potato disks and roots of *Vicia Faba*. She found that the hydrogen ion is rapidly absorbed from dilute acid solutions by living tissues, and concluded that the anion, particularly in organic acids, plays a large part in determining the effects of the acid on protoplasm. In the case of the mineral acids, HCl, HNO_3, and H_2SO_4, the stronger solutions can penetrate the cells for a time without causing much injury as measured by exudation of electrolytes; but organic acids like formic and acetic cause very rapid increase in conductivity, due to exosmosis of electrolytes from the cell. With these two acids there is first a decrease and then after a few hours a very noticeable increase in H^+ ion concentration. This is thought to be due possibly to the production of acids within the tissues which diffuse out through the altered plasmatic membrane.

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[12] DELF, E. MARION, Studies of protoplasmic permeability by measurement of rate of shrinkage of turgid tissues. I. The influence of temperature on the permeability of protoplasm to water. Ann. Botany **30**:283–310. 1916.

[13] HIND, MILDRED, Studies in permeability. III. The absorption of acids by plant tissue. Ann. Botany **30**:223–238. 1916.

As to the mechanism of absorption, a few experiments furnish evidence favoring the idea that the plasmatic proteins rather than the lipoids are active in the acid absorption.

A very important paper by STILES and JØRGENSEN[14] challenges not only the theory of permeability proposed by CZAPEK some years ago, the surface tension theory, but also all the facts and assumptions upon which that theory was founded. Because of its greater exactness and more general applicability to a study of all kinds of plant tissue, the Kohlrausch electrical conductivity method of estimating osmosis of electrolytes was used as a means of measuring changed permeability. Disks of potato were placed in non-electrolytic reagents of such strength as to produce irreversible changes in the protoplasm. Exosmosis of electrolytes was measured in the presence of a number of homologous monohydric alcohols, chloroform, chloral hydrate, ether, urethane, acetone, aniline, and pyridine. In all cases corrections for the depression of conductivity caused by the presence of the non-electrolyte in the external solution were made. In every case the rate of exosmosis was found to depend upon the concentration of the substance in solution in contact with the disks. The higher the concentration the more rapid the exosmosis, and CZAPEK'S observation that any member of the homologous series of primary alcohols has a greater effect on osmosis than a lower member of the series, if of equimolecular concentration, is confirmed. No such thing as a critical concentration, however, below which exosmosis did not occur and above which it did occur, could be found. Exosmose of electrolytes occurred in all concentrations used, down to mere fractions of the critical concentrations for exosmosis found by CZAPEK'S crude methods. The rate of diffusion of electrolytes was found not to be a function of surface tension alone. If the critical concentration of isobutyl alcohol were to be taken as 0.3 M. and the other alcohols compared with it as to equal exosmosis in a given time, the surface tensions of the various alcohols do not agree at 0.68 of the surface tension of water, as CZAPEK stated, but vary from 0.79 in methyl alcohol to 0.59 in isoamyl. The higher the alcohol the greater the lowering of the surface tension required to produce a given amount of exosmosis in a given time. Each item of evidence and the whole tissue of assumptions upon which CZAPEK built his theory of the plasmatic membrane is considered in detailed fashion and without gloves. The authors reject each point and assumption as untenable. In their own words, "from this review of the details of Czapek's work on the plasma membrane, it is clear that neither the experimental evidence nor any part of the theory based upon it can be accepted." They have sought to apply the law of mass action to the rate of osmosis in cases of permeability involving irreversible changes in the protoplasm, and a mathematical expression has been deduced connecting the time

[14] STILES, WALTER, and JØRGENSEN, INGVAR, Studies in permeability. IV. The action of various organic substances on the permeability of the plant cell, and its bearing on CZAPEK'S theory of the plasma membrane. Ann. Botany **31**:47–76. 1917.

element with exosmosis. Curves representing the equation derived thus on theoretical grounds resemble in type those obtained in actual experiments. The methods used in this work seem admirably adapted to a crucial test of CZAPEK's theory, which seems entirely untenable in view of the evidence submitted.—CHARLES A. SHULL.

Desiccation.—An investigation of the course of desiccation and partial starvation in cacti has been made by MACDOUGAL, LONG, and BROWN.[15] The principal studies center upon the changing rate of water loss, chemical changes in the food reserves, plasmatic colloids, and cell sap, and the morphological changes which occur during long periods of desiccation. In one case a large *Echinocactus* was under observation for 6 years after removal of the plant from the soil. Water loss is rather rapid at first, but proceeds more and more slowly with time. While 10 per cent of the water was lost the first year in one specimen, during the sixth year only 5 per cent of the water remaining at the beginning of that year was lost. The loss of water is much more rapid of course in the open than in diffuse light and *Echinocactus* can withstand desiccation not more than 2 years with free exposure.

The chief chemical changes noted during the starving period concern the carbohydrates. The density of the cell sap decreases, due to disintegration of the carbohydrates, and the reducing sugars are found mainly in the inner part of the cortex in desiccated specimens rather than near the surface as in normal plants. The total amount of reducing sugars decreases during desiccation, while non-reducing sugars are increased noticeably in the cell sap. Reduction of the amount of sugars leads to reduction of acidity if the light intensity is sufficient for photolysis of the acid. In weak light even, if the sugars run low, the acids may accumulate because of the absence of photolysis. Differences in acidity are thought to be partially responsible for differences in the colloid hydration and swelling of tissues when placed in water.

The main morphological changes consist in thickening of the cuticle, thinning of the anterior walls of the guard cells, partial destruction of the plasmatic colloids, shrinkage in the size of the nucleus, and especially the development of cortical lacunae through hydrolysis of the cell walls of this region of the stem. The vascular tissues are not affected, and the medullary cells much less than the cortical cells.—CHARLES A. SHULL.

The vegetation of Michigan.—From the data obtained during a few weeks in Michigan, HARPER[16] has listed the principal plants in the order of their abundance and has discussed certain features of the environment. He recognizes but two types of succession, the one from the filling up of lakes and other

[15] MACDOUGAL, D. T., LONG, E. R., and BROWN, J. G., End results of desiccation and respiration in succulent plants. Physiol. Res. 1:289–325. 1915.

[16] HARPER, R. M., The plant population of northern lower Michigan and its environment. Bull. Torr. Bot. Club 45:23–42. 1918.

depressions, and the other that following fire. In connection with the former, he distinguishes the usually recognized types of marsh and bog vegetation and states that the main distinction between the two is in the rate of growth, the slow rate of growth in bog plants being largely explained upon the basis of a dearth of mineral plant food in the substratum, which is also supposed to account for the presence of the same species upon the uplands in colder climates. No experimental evidence is given in support of this explanation. It is also rather surprising to be told that bog vegetation is "sometimes erroneously called xerophytic," after the almost endless discussion of bog xerophytes.

A deficiency of mineral plant food is also given as an explanation of the slow progress toward mesophytism of the pine forests upon sandy uplands. Leaching is supposed to prevent the accumulation of any considerable amount of plant food near the surface of the ground. This may possibly hold for the sandy plains, but if so it is difficult to see why it should not also apply to the pure sand of the dunes, where mesophytic forests develop rather quickly and where the conifers are soon largely replaced by deciduous species.

In discussing the influence of fire upon forest establishment, the error is made of stating that the cones of *Pinus Banksiana* remain closed and attached to the tree for many years, opening and discharging their seed after burning. Closer observation would have shown that the cones that remain for several years upon this pine open and discharge their seed very promptly upon ripening, and that the tree is in no wise dependent upon fire for its seeding.—GEO. D. FULLER.

Fairy rings and their effect on vegetation.—Of more than ordinary interest is a recent paper on fairy rings by SHANTZ and PIEMEISEL.[17] Before taking up their own researches, they present an excellent summary of past studies and theories concerning them, as well as a table of the fungi that have been reported as being responsible for rings. Some fungi, as *Agaricus tabularis*, are very destructive to grass and other vegetation; some, as *Calvatia* and *Lycoperdon*, are beneficial; and some, as *Lepiota*, have little effect of any sort. Striking conclusions are given relative to the age of rings. The conditions in eastern Colorado are not very favorable, either for spore germination or mycelial advance; in favorable years there may be a mycelial advance from the ring center of 30–60 cm., as compared with almost no advance at all in dry years. Some of the rings are very large, and from the growth measurements that have been made, a few are estimated to be 400–600 years old. Where vegetation is stimulated, it was concluded from careful study that this is due to the reduction of nitrogenous organic matter to available nitrates and ammonia salts, and to the subsequent decay of the fungous filaments. Deterioration or death of vegetation are attributed mainly to drought, caused by the prevention of water

[17] SHANTZ, H. L., and PIEMEISEL, R. L., Fungous fairy rings in eastern Colorado and their effect on vegetation. Jour. Agric. Research 11:191–246. *pls. 21. figs. 15.* 1917.

penetration by the masses of fungal filaments. Vegetation thus destroyed is replaced, after the death of the fungous, first by weeds, then by short-lived grasses, and eventually by the original short-grass cover.—H. C. COWLES.

Foreign pollen on Cycas.—It is well known that in some cycads the ovules reach the maximum size for the species whether pollination has occurred or not; while in others the ovules, if not pollinated, soon disorganize. *Cycas Rumphii* belongs to the latter category.[18] Female plants of this species are very abundant in Ceylon, but no male plants have been observed for several years. In localities where male cones of *Encephalartos* and *Macrozamia* are abundant, the pollen of these species germinates in the pollen chamber of *Cycas Rumphii* and causes the ovule to develop to the full size. Since the pollen of cycads germinates readily in artificial solutions, it is not strange that pollen of one species should germinate in the pollen chamber of another. In this case, however, no fertilization takes place, and mature seeds, which should show the embryo in an advanced stage of development, showed no trace of an embryo. A few years ago the reviewer pollinated *Stangeria* with *Zamia* and obtained three large seeds, which were planted but failed to germinate. It is possible that the pollen stimulated growth but failed to fertilize the egg, so that, as in *Cycas Rumphii*, no embryo was produced.—CHARLES J. CHAMBERLAIN.

Water culture.—In a critical discussion of the water culture method of studying growth phenomena, STILES[19] calls attention to the limitations of the method. He points out the great complexity of the factors involved, and applies BLACKMAN'S idea of limiting factors. The difficulty of analyzing the results of such experiments, due to the interaction of so large a complex of factors, few of which, even those whose action is under investigation, can be controlled, is made clear. Some factors, as for instance the influence of the respiratory activity of the roots on the culture solutions, have been neglected in all water culture work. The variability of individual plants is so great that a large amount of labor is required to secure results even with a low degree of accuracy. Nevertheless, for certain kinds of problems it may be the only method available.—CHARLES A. SHULL.

Grasses of Illinois.—Miss MOSHER[20] has published a manual of the grasses of Illinois, recognizing 204 species in 63 genera, over one-fifth of the species being recorded for the first time as occurring in Illinois. The analytical keys, descriptions, and numerous text cuts make the bulletin very useful in the recognition of the grass flora.—J. M. C.

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[18] LE GOC, M. J., Effect of foreign pollination on *Cycas Rumphii*. Ann. Roy. Bot. Gard. Peradeniya **6**:187–194. *pl. 13*. 1917.

[19] STILES, WALTER, On the interpretation of the results of water culture experiments. Ann. Botany **30**:427–426. 1916.

[20] MOSHER, EDNA, The grasses of Illinois. Univ. Ill. Agric. Exper. Sta. Bull. 205. pp. 261–425. *figs. 287*. 1918.